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BIRD SPECIATION ON THE AUSTRALIAN CONTINENT

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CONTENTS

I. INTRODUCTION

This work is a study of vertebrate speciation on a continent. It seeks to understand the nature of the various forces operative in Australia, including the barriers breaking up distribution and leading to the isolation and divergence of populations. A quantitative approach is used to determine the number of new species currently evolving and the "potential" of the continent for producing further species.

Our basic knowledge of the speciation process has been derived from the study of the faunas of archipelagos and the many striking illustrations to be found there provide the classic examples. Continents, lacking the more bizarre intermediate forms and obvious distributional barriers (e.g. areas of sea), present a much less convincing case for geographic speciation. Thus, notwithstanding various fine studies, one school (Goldschmidt, 1940, p. 183) categorically denies that the infraspecific variation that is such a feature of continental populations can be an intermediate step in the formation of new species. Such variation, it is maintained, is "dead end" and of a purely local adaptive nature. A large number of clear-cut examples of continental speciation and the circumstances surrounding them are detailed here and explained. In order, moreover, to arrive at a quantitative comparison of the potential of archipelago and continent for giving rise to new species, the number of morphologically differentiated, isolated forms in Australia and an archipelago area of equivalent size are calculated.

It is now generally accepted that the successive steps leading to the completion of speciation are as follows:

(a) Part of an individually variable population becomes spatially isolated from the parental stock.

(b) Under conditions of isolation it diverges genetically, ecologically, physiologically, and morphologically.

(c) The differences become increasingly great.

(d) Finally, the isolates become so different from each other that they can no longer successfully interbreed, i.e. they are reproductively isolated. The ultimate proof of this, of course, is only forthcoming in those cases when, under natural conditions, the two forms secondarily come together and do not interbreed.

Mayr (1950a) has listed some of the proofs for geographical speciation as follows: (a) the occurrence of geographic variation in species characters; (b) the existence of borderline cases between subspecies and species; and (c) "circular overlaps," that is, cases where the end members of a chain of interfertile races meet and do not interbreed. Recently completed speciation is indicated by examples of: (a) double invasions, (b) superspecies, (c) marginal overlaps of closely similar species without interbreeding. Of particular significance also is the occurrence of allopatric hybridization, the result of a premature reuniting of differentiating isolates (i.e. before specific distinctness has been reached).

The approach in the present instance is to investigate the occurrence of intermediate stages in the speciation process and their frequency, and to seek and detail cases of the important associated phenomena. Each species has been studied to determine if it is monotypic or if geographic variation (clinal or in association with isolation) occurs. Isolates are graded according to the degree of their differentiation, and the total number for each species, family, and ecological subdivision calculated. The significance of various aspects of species ecology on variation and speciation, in particular the vegetation formation (habitat) occupied and nature of seasonal movements, is treated in detail.

Four hundred and twenty-five of the 531 breeding land and freshwater bird species and semi-species occurring in Australia (80 per cent of the total) are included in the present study.

II. MATERIALS AND METHODS

The present work was initiated in the period 1953-1955, when the writer was a Fulbright scholar at Harvard University. The basic material is from two sources: (a) systematic studies by the author (245 species) and, (b) recent taxonomic reviews, i.e. by workers using the "new systematics" (180 species). The bulk of the writer's work was carried out on the bird collections of the American Museum of Natural History, New York, which are easily the world's most comprehensive for the Australian and Pacific regions. They now include the Rothschild Collections and the bulk of the Mathews types, as well as much recent material from Queensland (J. Henry) and Western Australia (K. Buller). Other U.S. collections examined were the Gould Collection in the Philadelphia Academy of Sciences, the Arnhem Land Collection (H. G. Deignan) in the U.S. National Museum, and recent Queensland collections (by K. Stager) in the Los Angeles County Museum. Following the writer's return to Australia, material in the Australian Museum, Sydney (including recent collections made by the author in New South Wales, central and northern Australia), National Museum of Victoria, Melbourne, and South Australian Museum, Adelaide, was incorporated into the study.

In the studies of geographic variation, standard taxonomic methods have been used (see author's various papers), in all cases the emphasis being on the population, not the individual.

Published taxonomic data used in the work were obtained from the following sources: families Podicipitidae (Mayr 1943);

Accipitridae, Falconidae, and Pandionidae (Amadon, 1941; Condon, 1951a; Condon and Amadon, 1954); Ardeidae and Threskornithidae (Mayr, 1943; 1945b; and Amadon, 1942; Amadon and Woolfenden, 1952); Anatidae (Mayr and Camras, 1938; Mayr, 1940a, 1945b; Amadon, 1943; Amadon and Woolfenden, 1952; Ripley, 1942); Rallidae (Peters, 1934; Mayr, 1949); Psittacidae (Condon, 1941; Mayr, 1951; Cain, 1955); Sittidae (McGill, 1948; Mayr, 1950b); Cracticidae (Amadon, 1951); Grallinidae (Amadon, 1950a); Ptilonorhynchidae (Mayr and Jennings, 1952); and the following genera: *Geopelia* and *Lophophaps* (Mayr, 1951) in the Columbidae; *Acrocephalus* (Mayr, 1948) in the Silviidae; *Pachycephala* (Mayr, 1954a); *Falcunculus* and *Oreoica* (Mayr, 1953a, b); *Orthonyx* (Mack, 1934a); *Gerygone* (Meise, 1931); *Malurus* (Mack, 1934b; Serventy, 1951); *Sericornis* (Mayr, 1937; Mayr and Wolk, 1953); *Acanthiza* (Mack, 1936; Mayr and Serventy, 1938) in the Muscicapidae; and *Zosterops lutea* (Mees, 1957) in the Zosteropidae.

In addition, the general study by Condon (1951b) on the birds of South Australia contains much basic taxonomic information.

Detailed studies of geographic variation were carried out by the author on the following: the families Turnicidae, Pedionomidae, Columbidae, Alcedinidae, Menuridae, Atrichornithidae, Campephagidae, Artamidae, Meliphagidae, Zosteropidae, Dicaeidae, Oriolidae, the subfamilies Estrildinae (Ploceidae) and Muscicapinae (Muscicapidae); and the genera *Megalurus* (Silviidae), *Climacteris* (Sittidae), *Orthonyx, Sphenostoma, Drymodes, Psophodes* (Cinclosomatini, Muscicapidae), and *Epthianura, Ashbyia, Smicrornis, Aphelocephala, Hylacola, Calamanthus, Cthonicola, Origma, Pycnoptilus, Cinclorhamphus, Amytornis, Dasyornis,* and *Stipiturus* (Malurini, Muscicapidae). The majority of these studies have now appeared, or will later appear, as separate papers. Those so far published are: Oriolidae and *Megalurus* (Keast 1956a, b); *Aphelocephala, Dasyornis, Stipiturus,* Alcedinidae, *Climacteris* (Keast 1957a-e); Muscicapinae, *Amytornis, Epthianura* and *Ashbyia, Dicaeum,* Artamidae, Estrildinae, *Psophodes, Smicrornis,* Campephagidae (Keast 1958a-i).

A marked advantage of using birds for studies in speciation is that there is a great amount of data on distribution, habitat and general ecology available in the literature. This applies equally well in Australia. Included in the standard works consulted in the present study are: North, 4 vols. (1901-1914), Mathews, 12 vols. (1910-1927), Serventy and Whittell (1951), Mayr (1941, 1944a, 1945a), and the periodicals, *The Emu*, and *South Australian Ornithologist*, now in their 58th and 44th year of publication, respectively. Field workers in various parts of Australia have kindly made supplementary material available. In addition, the writer has had the advantage of having worked on the birds of eastern Australia over a number of years and to have made field trips as follows: central Queensland (1950, 1951), Bass Strait islands (1951), Kimberleys, coastal Northern Territory, and north Queensland (1952), Victoria (1951, 1955), central Australia (1952, 1958), southeastern South Australia (1958), western New South Wales, including the mallee regions (1956-1959), southwestern Australia and the Barlee Range (midwestern Australia) (1959). Besides acquiring taxonomic material, this has made it possible to check distributional limits, degree of attachment to habitat, aspects of seasonal movements, and to look at certain contact and hybrid zones.

Information on the Australian continent as an environment has been drawn from various official and other sources. In the case of the map showing former connections between Australia, New Guinea, and Tasmania, the 150 and 300 ft. isobaths are calculated from the sea depths shown on the Australian sheet of *Carte Generale Bathymetrique des Oceans*, 3rd Edition, 1942, Monaco. The map showing the limits of the Australian and Asian continent shelves is adopted from that in Mayr (1945c). Physiographic data are primarily from the 1942 Orographical Map of Australia by H. N. Warren, and Hills (1949). Data on temperature, rainfall, and associated factors, are from various official maps (undated), the Climatological Atlas issued by the Commonwealth Meteorologist (also undated), Leeper (1949), and the recently published Atlas of Australian Resources, Department of National Development, 1951-1955. The climatic map is based on the chart of Dr. J. Gentilli (undated). Other climatic maps, more precise and detailed, are to be found in Andrewartha and Birch (1954) and in the Atlas of Australian Resources, cited above. The maps of vegetation formations and soils are simplifications of those of Prescott (1931) and Wood (1949). Information as to Pleistocene and post-Pleistocene climates and vegetation changes is from Browne (1945), Crocker and Wood (1947), Gentilli (1949), David (1950), Fairbridge (1953), Crocker (1959a), and Wood (1959).

III. DEFINITIONS AND TERMINOLOGY

For the purposes of the present study it has been necessary to depart somewhat from the terminology normally used by taxonomists. This applies particularly to the dropping of the term "subspecies" or "race" which, as used, simply means a morphologically differentiated population and tells nothing of evolutionary potential. The emphasis here is on isolation and hence the term "isolate" is used. Where subspecies names come into the text, it is as a ready means of referring to a form that already bears a name in the literature.

Species: The modern biological definition for the species is followed, the criterion being reproductive isolation. Care is taken to draw attention to, and view somewhat differently, those species that are members of superspecies (i.e. that are allopatric representatives), and that fall into the category of "semispecies" (see Mayr, 1942). The latter are the distinctive isolates of uncertain genetic status that the taxonomist may call species because they have reached a significant stage of morphological differentiation and for the sake of expediency.

Isolate: This is a population or populations isolated from the main stock by a geographic barrier so that interbreeding is prevented. Isolates may be undifferentiated, slightly differentiated, moderately or well differentiated, the last-named being forms in which speciation is well advanced.

In calculations of the number of morphologically differentiated isolates one stock is set aside as the "parent" from which the isolates are diverging. For the sake of consistency, in comparisons between continent and archipelago, in those species that range through both, one form in each is set aside as "parental."

Species that do not vary geographically, or have only clinal variation, do not, of course, have isolates.

Population: This is used as an inexact term to mean simply the members of a species inhabiting a restricted area. It is credited with the morphological characteristics of a *series* of adult specimens from that area.

Morphological characters: Those used are variation in colouration and colour-pattern, the dimensions of the appendages (wing length [a good criterion of over-all size in birds], bill length, tail length) and, sometimes, the ratios of the length of one appendage relative to another. The term "morphological" is used to stress the fact that it is the variation visible in the preserved specimen that is being considered.

Hybrid zones: These are characterized by the presence of very variable populations, with extreme types, as well as a range of genetic recombinants being present. Most are narrow but in some cases a rather broad zone of intergradation occurs.

Hybrid zones mark the breakdown of a former barrier and the reunion of isolates that had reached a marked degree of morphological differentiation. A minor amelioration of climate in Australia, and in some cases human interference with habitat, is enabling various species to extend their range at the present time. Only a minority of them, however, have as yet contacted their geographic counterparts to form hybrid zones or zones of overlap.

Stepped clines: The presence of a "step" in a cline is evidence of former isolation and there are good examples of this phenomenon in a few Australian bird species, e.g. *Pachycephala pectoralis* (Mayr, 1954a). Minor zones of intergradation that may not, or do not, indicate secondary junction (note also the remarks of Miller, 1955) are discussed separately.

Continuous clines, though they may involve peripherally adapted forms that could diverge rapidly if isolated, do not form a stage in the speciation process. Hence they receive only passing attention.

Barrier: This is an area within, or at the edge of, the range of a species where it cannot thrive because of its innate ecological limitations. The term is used here strictly as a geographic or spatial concept.

The well defined distributional barriers, especially those that have given rise to distinctive isolates, are the critical ones here.

Habitat: This term is used in a broad sense to mean the basic vegetation formation occupied by a species.

About ten vegetation formations are of major importance to Australian birds: rain forest (under which may be included monsoon or pseudo-rain forest), sclerophyll forest, savannah woodland, savannah grassland, mulga, mallee, desert (spinifex) grassland, gibber desert, mangroves, and swamps and rivers. The majority of bird species occur in only one, or are common in only one, of these formations, sometimes being restricted to a specialized sector, association or sub-association within it (e.g. plateau-top heathland within the eastern sclerophyll sector). Habitat specificity is discussed in Section VI.

The significance of the vegetation formation in bird distribution and speciation lies, of course, in the fact that it represents a zone of relative physical and biological constancy. It is to these grouped factors that species have adapted and specialised during their development. "Habitat" is as valid a species character as morphological or genetic criteria, in most cases.

Refuge: This term refers to fertile or semi-fertile areas, mostly mountainous or hilly sections, in which plants and animals have been able to persist during arid periods.

Australia is currently in an arid phase, with marked aridity stemming from the early Recent. The rain forest, sclerophyll forest, and savannah woodland areas of the continent are today broken up into a disconnected series of peripheral segments, some of vast extent. Use of the term "refuge area" should not carry the inference that species "retreated" into them with the onset of aridity, but that only the stocks inhabiting those areas were able to survive.

Sedentary or resident species: This refers to a species the members of which do not undertake seasonal movements but, as adults at any rate, spend the year in the general vicinity of their breeding territories. There is a minimum intermixture of individuals from the different parts of the species range in this group.

Migratory species: This term is used for species that have a south-north migration and regular breeding areas. They are typically inhabitants of the better watered coastal forests where conditions are uniformly good. Examples: *Coracina novaehollandiae* (eastern Australia) and *Artamus cyanopterus.*

Nomadic species: This term denotes those species that: (a) undertake extensive group movements of irregular amplitude and direction and, (b) breed wherever conditions happen to be suitable, e.g. *Epthianura tricolor* and *Histriophaps histrionica.* (See also Section VI).

Nomenclature: That of Mayr and Amadon (1951) is followed in the present work. The species order is that of the 1926 Checklist of the Royal Australian Ornithologists Union.

IV. THE AUSTRALIAN CONTINENT AS A BIOTIC ENVIRONMENT.

The Australian continent has a land area of 2,984,000 square miles, about three-quarters of that of Europe (including European Russia). It is approximately the same size as the United States and is some twenty-five times the land area of the British Isles. It has been a stable land mass for a considerable portion of its geological history and Archaean rocks outcrop over an extensive area.

Australia differs from the other continents in various ways including:

(a) Spatial isolation from other large land masses (Figs. 1,

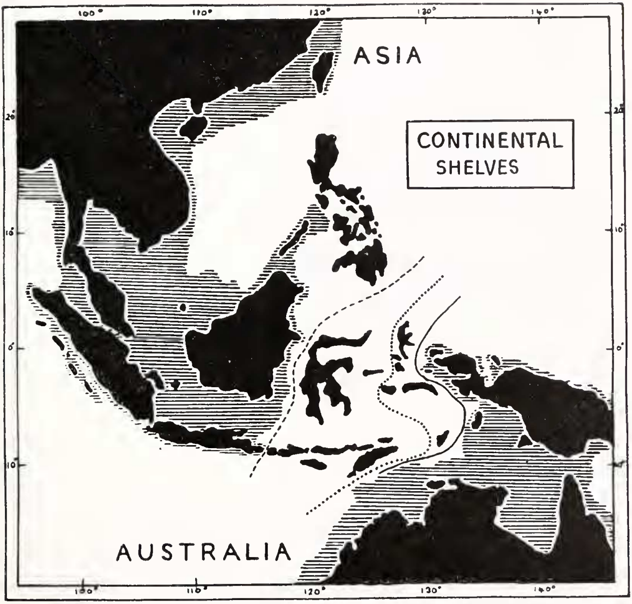

Fig. 1. Australia in relation to Asia, and showing limits of continental shelves (100 fathoms or 600 foot line). The dashes indicate Wallace's Line (original), the dots Weber's Line, and the continuous line the western limits of the Australo-Papuan continental fauna.

At the height of Pleistocene glaciation the sea level only fell 300 feet. The cross-hatched areas nevertheless correspond fairly well with the extent of land at that time. (Figure modified from that in Mayr, 1945c).

2).

(b) General flatness, mountain barriers to dispersal being virtually nonexistent (Fig. 3).

(c) Absence of areas of extreme cold, the winter snowbelt amounting to only a few hundred square miles. There are no permanent glaciers or snowfields. The over-all climate varies from subtropical to cold temperate. The mean annual temperatures range from over 80°F. in the tropical north down to 45°F. in the highlands of the south. Daily minimum temperatures for July (coldest month) are 60-70° and 30-45°F. respectively, and daily maximum temperatures for January (hottest month) are 85-90° and 60-65°F., respectively.

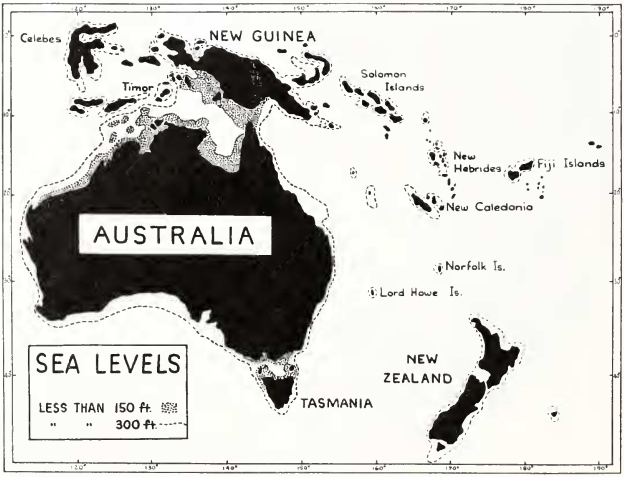

Fig. 2. Australia in relation to the islands to the north and east. The stippled areas indicate the land extensions that would follow a 150 foot drop in sea level, and the dashes show the 300 foot line. Tasmania and New Guinea were twice connected with Australia during the Pleistocene when the sea level fell 300 feet.

Deep water isolates Timor, New Zealand, and the islands to the east and separates New Britain from New Guinea.

(d) Generalized aridity. Agriculturists classify Australia as being only one-third fertile, with the remaining thirds semi-arid and arid, respectively. Rainfall (Fig. 4) is the all-important factor governing the distribution of life in Australia.

(e) The arrangement of the basic vegetation formations (which form the bird habitats) into broad parallel, north-south (mostly), or east-west zones (Fig. 5). The altitudinal zonation of plants and birds that is such a feature of the Rockies and other high mountain regions of the world is virtually absent in flat Australia.

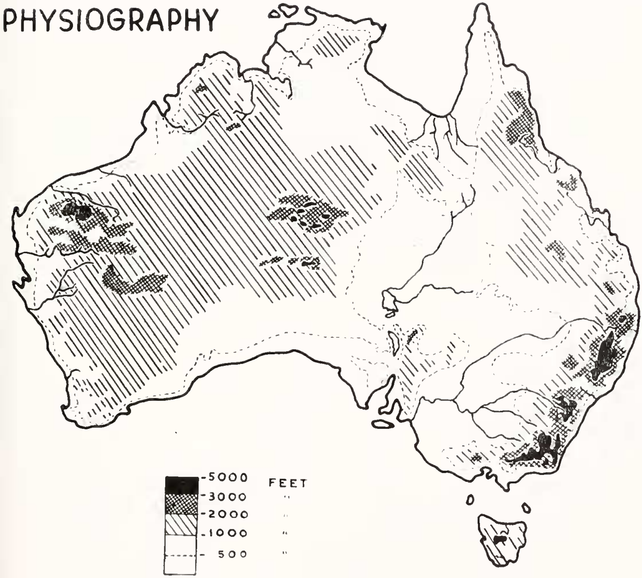

Fig. 3. Physiographic map of Australia. The continent is relatively flat. Mountains are not, per se, significant barriers to avian distribution. Their control of distribution, by way of rainfall and vegetation, however, is profound.

The dotted line indicates drainage patterns. (Map redrawn from that of Hills, 1949).

Physiography, Climate and Vegetation

Physiography: The continent falls into three physical subdivisions (Fig. 3): the Great Plateau or Archaean Shield that covers the western half of the continent, the Central Basin, and the Eastern Highlands (Hills, 1949; David, 1950). The backbone of the last-named is the Great Divide, the range that extends southwards down the full length of the east coast, thence to Tasmania and westwards to central Victoria. It is by far the most significant physiographic feature on the Australian continent and not only influences climate and vegetation over a wide area but permits a richness and diversity in the flora and fauna that would otherwise be impossible. Nevertheless, only relatively

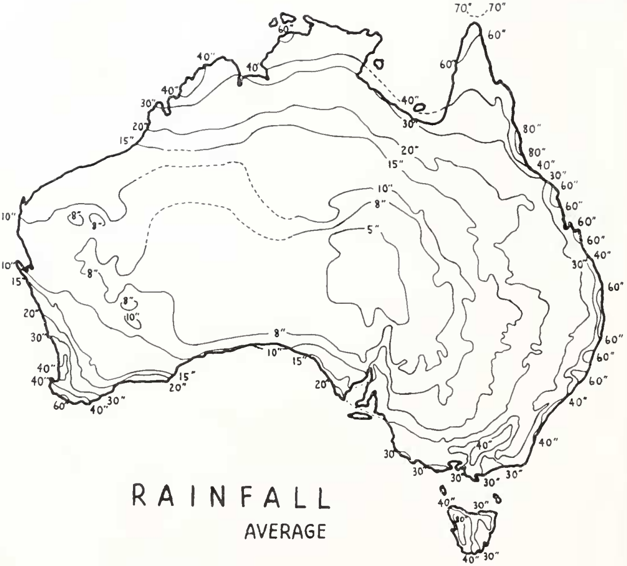

Fig. 4. Rainfall of Australia (average annual figure in inches). The pattern is one of concentric zones of increasing rainfall outwards from an arid central area. The desert extends to the coast in the south and west. The eastern, southeastern, southwestern sections, and a small area in the north, are fertile.

(Map adapted and simplified from that in the Atlas of Australian resources — Rainfall; Published by the Department of National Development, 1952.)

restricted parts of it exceed 4000 feet in height and the highest peak in Australia, Mount Kosciusko in the southeastern section, is a mere 7,300 feet in height.

Here and there over the surface of the continent, elevated areas, residual masses, and dissected plateaux take the form of mountain ranges. Amongst the most interesting of these from the faunistic viewpoint are the Mount Lofty and Flinders Ranges in South Australia, the Macdonnells and other ranges in central Australia, the Darling Scarp and Stirling Ranges in the southwest, Hamersley Ranges and the Kimberley district in the northwest of the continent (Fig. 3). Though typically these do not rise more than a couple of thousand feet above the surrounding plain they have a marked local influence on rainfall and vegetation and

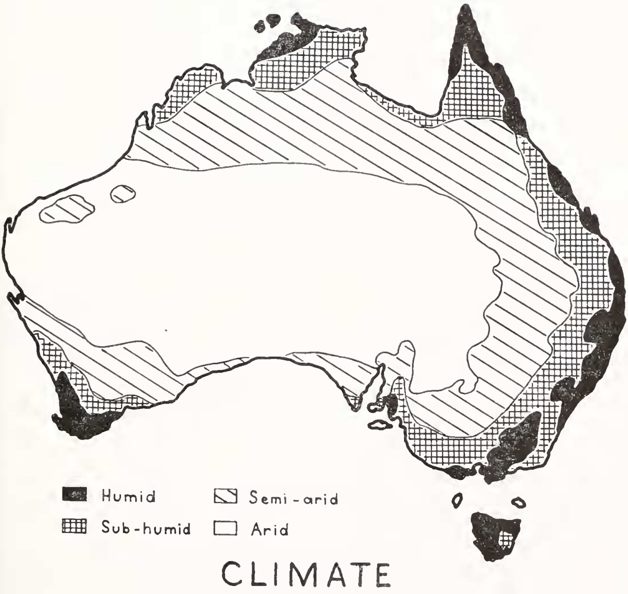

Fig. 4a. A simplified climatic map of Australia. Derived by J. Gentilli (Thornthwaite formula).

permit the existence of various forms of life that would otherwise be impossible.

Rainfall: The rainfall patterns of Australia will be seen from the map of average rainfall (Fig. 4). The isohyets take the form of concentric zones of increasing rainfall extending outwards from an arid interior. The transition is particularly well defined in the east where the belts extend from north to south parallel with the coast. In places, tongues of dry country extend through from the interior to the coast, breaking up the more fertile country into sectors.

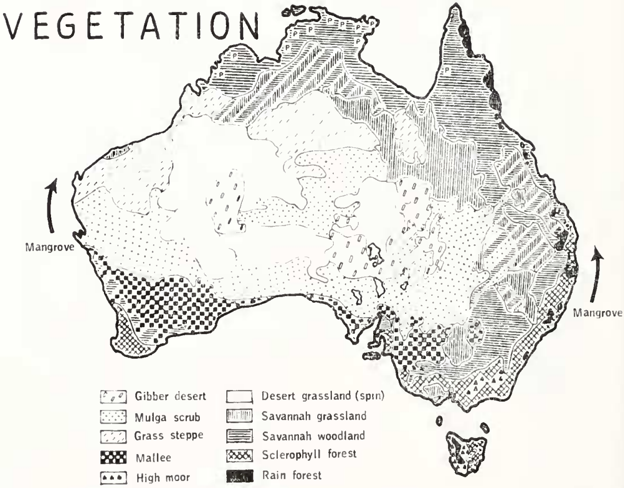

Fig. 5. Major vegetation formations of Australia, simplified from Prescott (1944) and Wood (1949). For explanatory notes see Table 1. There is a close relationship between the distribution of bird species and that of the major vegetation formations, with gaps in the formations acting as isolating barriers. M = mangroves; P = pseudo-rainforest (riverside).

Two main systems operate to produce the Australian rainfall, a winter one that moves up over the southern part of the continent (the "Antarctic System") and a summer one (the "Tropical System") that brings monsoonal rains to the north of the continent. The north of the continent has a wet summer and a dry winter, whilst in the south the reverse is the case. Since, however, the summer is hot in the north the rainfall there is less effective and the over-all climate is dry. The Eastern Highlands ensure that the east and southeast of the continent benefit both from the summer and winter systems and have a comparatively even rainfall. The central regions of the continent are towards the limits of penetration of both systems, either or both of which may fail. The 10-inch line in the south and 15-inch zone in the north outline the limits of the desert.

Other facets of rainfall in Australia are its unreliability over large sections and the high rate of evaporation, factors greatly influencing plant growth. The irregularity of the rainfall in the interior explains the high proportion of nomads in the avifauna there.

The climatic zones in Australia (Fig. 4a) reflect the rainfall picture.

Vegetation: The basic vegetation zones occurring on the Australian continent and a summary of their characteristics, are set out in Table 1. The approximate area of the continent covered by each (author's calculations) is given in Table 2. The close link between rainfall and the distribution of the basic vegetation formations in Australia will be seen from a comparison of Figures 4 and 5.

Rain forest is restricted to the eastern seaboard and is broken up into pockets. Sclerophyll forest, eastern and southern in distribution is also largely restricted to the coastal regions and is discontinuous.

Savannah woodlands occur as broad tracts across the north and down the east of the continent (mainly).

Savannah grasslands, mulga, and spinifex desert (desert grassland) are the semi-arid to arid country formations. They occur as broad and continuous zones with the latter two occupying the central areas.

Mallee, a stunted but floristically diverse formation, occurs in broad southeastern and western tracts (with some discontinuity) in the dry southern inland of the continent.

Mangroves extend practically right around the Australian continent but the rich and diverse tracts that support specialized mangrove bird species are restricted to the northernmost two-thirds. The swamps and marshes (not shown because of their relatively small extent) and rivers (homes of the water-birds) are developed to by far the greatest extent in the better watered southeast of the continent (Victoria and New South Wales). Even so, a good proportion of them are temporary.

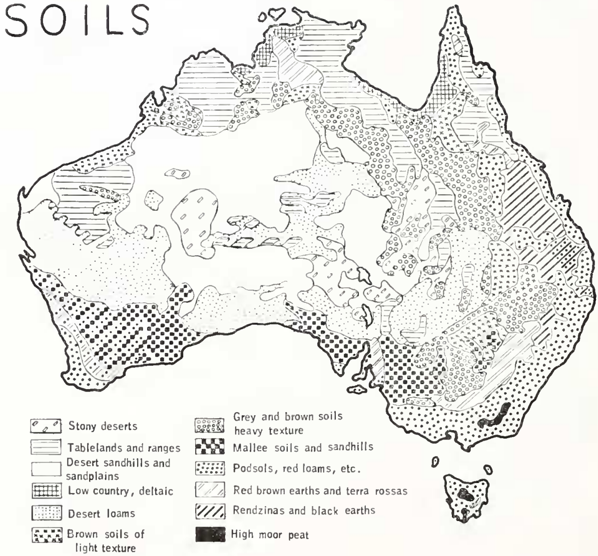

Fig. 6. The soils of Australia. Map is a simplified version of that of Prescott (1944), reproduced by Taylor (1949). Definitions of soil types are given by R. Crocker (see Keast, 1959a).

Physiography, rainfall, and soils, control the distribution of vegetation.

Soils: The major soil types occurring in Australia will be seen in Figure 6. The characteristics of these have been summarized by Crocker (*in* Keast, 1959a). Attention to the fact that the zonal soil groups in Australia follow a pattern somewhat similar to rainfall has been directed by Wood (1959). Again, there is a broad, but not absolute, zonal sequence and correspondence between soil type and vegetation.

Soil history in Australia, and its influence on bird distribution, through the vegetation, will be discussed in Section XI.

Spatial Relationship of Australia to other Land Masses

The distance between Australia and the nearest point of the Asiatic mainland today exceeds 2000 miles. This isolation dates back to the beginning of the Tertiary, a period of some 50,000,000 years.

The limits of the Australian and Asian continental shelves (100 fathom or 600 foot line) will be seen on Figure 1. The former, it will be noted, extends out for only a short distance but the latter includes Borneo and Java, over one-third of the distance towards Australia. During the Pleistocene emergence the sea-level is believed to have twice fallen some 250-300 feet, and it is obvious that the Asian continent must have extended a considerable distance towards Australia. Nonetheless, the faunistic differences between the two continents have been preserved. This underlies the significance of the intermediate deep-water gap, the islands within which have been highly unstable geologically. These islands, moreover, are "ecologically impoverished" and apparently only capable of supporting a somewhat limited number of bird species. On these grounds also they represent a "distributional bottleneck." A discussion of Wallace's Line is beyond the scope of the present paper. Several recent authors have, however, reviewed its zoogeographic significance; these include Scrivenor et al. (1943), Mayr (1945c), and Darlington (1957).

The islands adjacent to the Australian continent and their history are as follows:

Timor: This lies some 350 miles to the northwest of Australia, a gap that was narrowed to perhaps 50-70 miles at the height of the Pleistocene emergence. As will be seen from Figure 1, however, there is a narrow tract of deep water immediately to the east of Timor. The avifauna of Timor is a blend of species of western and eastern origin (Mayr, 1944a).

New Guinea: This large island is only 100 miles from Australia at its closest point. The intermediate water is shallow, extending down to only about 30 feet in the section to the north of Cape York. New Guinea has repeatedly been in direct contact with Australia. This was the case during part of the Tertiary and on two separate occasions in the Pleistocene.

New Caledonia: This island, 750 miles to the northeast of Australia, is separated by deep water and its isolation is of long standing.

New Zealand and Lord Howe Island: These islands lie, respectively, 1200 and 350 miles to the east of Australia. Both are regarded by geologists as "continental remnants," though a submarine trough extending down to 12,000 feet isolates New Zealand today. The nature of any pre-Tertiary connections with Australia are, however, highly speculative.

Tasmania: This island lies about 140 miles off southeastern Australia but with islands half-way across, and has a purely Australian fauna. Intermediate ocean depths only extend down to perhaps 150 feet and, like New Guinea, Tasmania was directly connected to Australia during part of the Tertiary and Pleistocene.

The influence of the surrounding land masses on the Australian avifauna has obviously been relatively slight, a fact that makes the continent ideal for speciation studies. Not only is the continent surrounded by areas of deep sea but, if Tasmania be included with Australia, only to the north has there been "interference" from outside. New Guinea has, however, continuously contributed new bird species to Australia.

V. THE AUSTRALIAN AVIFAUNA

Australia is credited with 707 species of birds by the Official Checklist of the Royal Australasian Ornithologists Union (1926). The recent treatment of Mayr and Serventy (1944), however, rightly reduces the number to some 651 species. There are 37 species of breeding seabirds, 83 visitors, 531 land and freshwater birds (29 of which come into the category of semi-species), with 14 being restricted to adjacent islands. It is on this total of 531 species that the calculations in the present work are based.

In accord with its being the smallest land mass, Australia has less bird species than the other continents, as the following figures of Stresemann (1927-1934) will show:

Australia	531 species
Africa	1,750
South America	2,500
North America	750
Palearctic region (Europe and Asia)	1,100

The tropical island of New Guinea, immediately to the north of Australia, with only one-tenth of the land area, but dominated by tropical rain forest and high mountains, has no fewer than 509 species of land and freshwater birds, together with 28 semi-species, and 29 inhabiting adjacent islands, a total of 566 species. Thus it has a richer avifauna than Australia. If the 191 species common to both be eliminated, the combined total for Australia and New Guinea is 906, a sum that brings the section more into line with the major land masses of the Northern Hemisphere.

The Australo-Papuan region is one of the major zoogeographic subdivisions of the world and, in conformity with its peculiar mammalian, amphibian, and freshwater fish fauna, is rich in endemic bird families, subfamilies, and genera. In contrast with some lower vertebrate groups (freshwater tortoises, hylid frogs), various invertebrates and some plants, and despite the occurrence of flightless ratites, numerous parrots, etc., on both, Australia has no close affinities with the avifauna of South America. Likewise, supposed direct relationships with certain African elements (e.g., between *Promerops* and the Australian Meliphagidae) are now open to question (Mayr and Amadon, 1951). Many bird families do, however, extend from Asia to Australia, and some from Africa or Europe, through Asia, to Australia. Such may be equally well developed in both regions, e.g., Turnicidae, Campephagidae, Ploceidae, Zosteropidae. More commonly, however, only one or two species of such Palaearctic or Oriental families extend to, or occur in, Australia: Meropidae, Pittidae, Timaliinae, Sylviinae, Motacillidae, Nectariniidae, Coraciidae, Sturnidae, Oriolidae, Dicruridae. Avifaunal interchange across Wallace's Line and down the ''impoverished'' Indonesian island archipelago has been discussed by Mayr (1945c), Darlington (1957), and others.

The families and subfamilies endemic to the Australo-Papuan region have been listed by Darlington (1957) and Keast (1959b). Those occurring in Australia proper, and the number of species comprising each family, are as follows: Casuariidae (cassowaries), 1; Dromaeidae (emus), 1; Megapodiidae (incubator-birds), 3; Pedionominae (collared hemipodes), 1; Loriinae (honey lories), 6; Kakatoeinae (cockatoos), 10; Menuridae (lyrebirds), 2; Atrichornithidae (scrub-birds), 2; Malurinae (Australian warblers), 64; Meliphagidae (honeyeaters), 65; Cracticidae (Australian butcher-birds), 14; Grallinidae (mud-nest builders), 3; Ptilonorhynchidae (bower-birds), 8; Paradisaeidae, (birds of paradise), 3. Two hundred and thirteen species of Australian land and freshwater birds, or 35 per cent of the total, belong to these endemic groups. If, however, Australia and New Guinea be grouped together, with their total of 906 different species, the number of species belonging to these groups is found to reach 369 (41 per cent).

In addition to endemic families and subfamilies Australia has various endemic genera belonging to cosmopolitan families such as the Anatidae (ducks), Columbidae (pigeons), and Ploceidae (finches). The Strigidae (owls), Cuculidae (cuckoos), Rallidae (rails), and others are each represented by various endemic species. In contrast to this, interestingly enough, a couple of cosmopolitan bird species extend to Australia, e.g., the owl *Tyto alba,* the falcon *Falco peregrinus,* and the grebe *Podiceps cristatus.*

Considerable radiation has occurred in the Australo-Papuan region in various cosmopolitan families. Thus, Australia now has 18 species of ducks and geese, 23 pigeons and doves, 51 parrots (though a proportion of these are lories and cockatoos), 10 kingfishers, and 12 cuckoos.

From the viewpoint of its origin, the Australian avifauna could be said to have been built up by a series of waves of colonization from the north over a prolonged period, or by successive colonizations superimposed upon the earliest elements. Isolation has been fairly complete throughout.

VI. THE SAMPLING OF THE AUSTRALIAN AVIFAUNA

Eighty per cent (425 out of 531 species) of breeding land and freshwater birds are covered.

The sampling of species in the present work, has been a random one. Only a couple of families of lesser importance are unrepresented. The proportion of species of New Guinea-Pacific and Australian origin in the sample approximates to that actually occurring, as does the proportion of species with the different kinds of distribution in Australia, e.g., southern as against northern, peripheral and inland, extensive and restricted. The ratio of species inhabiting the various basic vegetation formations and of those falling into the various categories of seasonal movement is likewise maintained in the sample.

In the following, stress is placed on the relationship between speciation and (a) the phylogenetic group (i.e. family) to which a species belongs, (b) the vegetation formation it occupies, (c) the nature of its seasonal movements.

Sampling According to Classification and Family Categories

The classification and subdivisions of the Australian land and freshwater bird fauna are set out in Table 4. The number of species in each family and sample used in the present study are shown in the first column. Thirty-one families are covered in toto whilst some 90 per cent of the Muscicapidae and more than half the parrot species are included. The only important families unrepresented are the Strigidae (8 species), and Cuculidae (11 species).

Sampling According to Habitat (Vegetation Formation) Occupied

The major vegetation formations occurring in Australia, and the approximate continental area covered by each plus its percentage of the whole, are set out in Table 2. In succeeding columns the number of bird species restricted to or reaching its greatest abundance in each formation are shown, together with its percentage of the total avifauna. The final column represents a calculation of the number of square miles of habitat per species, to give a figure for the relative richness of each vegetation formation.

The sample of each type used as the basis for all the calculations in this work is set out in the first column of Table 5.

Savannah woodland, savannah grassland, mulga, and spinifex desert, cover the largest areas of the continent. By contrast, rain forest and mangroves, though covering only a small area, are richest, on the one hand, in terms of number of bird species and, on the other, in number of species per square mile of habitat. The largest number of species, however, could be said to be specialized for life in sclerophyll forest and savannah woodland. This figure, it should be noted, does not represent the number of bird species that could be seen in a day's observation in a typical area of each habitat, for in a savannah woodland, particularly, there is a relatively greater geographic replacement of species as between the north (tropical savannah) and the south. Rather, it expresses the number of species that are, basically, inhabitants of each.

In the compiling of Table 2, it was apparent that the avifauna of the more specialized vegetation formations, the rain forest, sclerophyll forest, mallee, desert (spinifex) grassland, mangroves, and swamps and rivers, tended to be fairly specific and conservative in habitat choice. Hence, little difficulty was had in allocating species to a category. This did not apply, however, to the more "transitional" types of vegetation formation: savannah woodland, savannah grassland, and mulga, which not only have much in common but interdigitate and overlap extensively. The dominant species in savannah grassland (or savannah woodland) may also be common in savannah woodland (or vice-versa) and

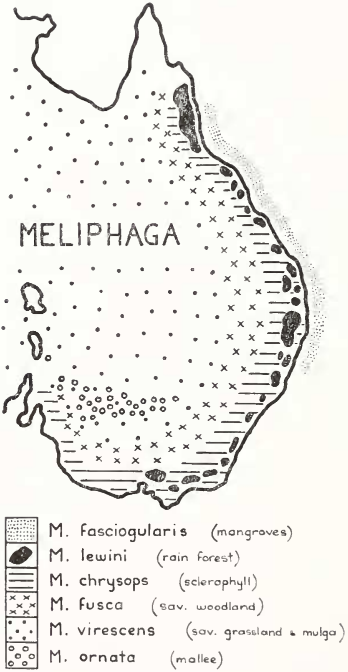

Fig. 7. Distribution of 6 species of the genus *Meliphaga* (honeyeaters) in eastern Australia to show correlation with major vegetation formations. The map is somewhat diagrammatic. Six species are inhabitants respectively of mangroves, rain forest, sclerophyll forest, savannah woodland, savannah grassland — mulga, and mallee.

This is an exceptionally good example of a phenomenon seen to at least some extent in most bird genera.

mulga, and penetrate the dryer sclerophyll forests and mallee. In these cases the alternative remained of creating several additional ''habitat categories'' or placing the species under the vegetation formation in which they were especially prominent. For the sake of simplification the latter course was chosen. The figures for savannah woodland and savannah grassland are placed in brackets in Table 2; they are probably relatively too high.

Apart from the above, a number of species occupy a life zone that is a continuum between two or more formations, e.g. the ''leafy canopy,'' mistletoe. Again, large hawks, crows, small aerial feeding species (e.g. swallows), and a few others, are little influenced by vegetation in their distribution. They have a range that is virtually continent-wide. For the sake of completeness these are included in whichever of the ''intermediate-type'' habitat categories they are especially prominent.

Each bird species is included only once in the calculations.

The whole problem of allocating species to habitat categories is much simplified in Australia, fortunately, by the basic vegetation formations being arranged in broad, parallel, zones.

Sampling According to Seasonal Movements

The seasonal movements undertaken by Australian land and freshwater bird species are complicated and every stage in the transition from one to another of the extremes is present. Thus, amongst the south-north migrants are species in which the movement is restricted to the more southern populations, or to a proportion of the individuals of these populations. In others the movement is entire. Amongst the nomadic species are some that are sedentary for a year or more, moving with the onset of a drought, and others that are nomadic in part of the range only. In the more typical nomads, however, the movements are general, irregular, occur frequently, and are of considerable amplitude. Many have, seasonally, a south-north bias to the movements.

For the purposes of the present work, species are broadly grouped into the three categories according to the nature of the seasonal movements over the bulk of the species range.

Grouped in this way, the Australian land and freshwater birds are as follows:

TABLE 7

	In Fauna		*In Sample*	
	No. of Species	% of Whole	No. of Species	% of Whole
Sedentary species	351	66	294	69
South-north migrants	42	8	32	8
Nomadic species	138	26	99	23

The small number of true migrants and the relatively great importance of the nomadic way of life on the Australian continent, as compared to the Palearctic and Nearctic regions, will be noted. Nomadism is an adaptation to unreliable and uncertain rainfall, though, in Australia, a certain amount of this behaviour is associated with the blossoming of food trees. Migratory species, in the restricted south-north sense in which the term is used here, are, as noted, mainly inhabitants of the well-watered eastern section of the continent.

VII. VARIATION AND SPECIATION IN THE VARIOUS BIRD FAMILIES

Order PODICIPEDES

Family PODICIPITIDAE

(Grebes)

There are three grebe species in the Australian region, only one of which is endemic. All have an extensive Australian range, are nomadic, and are swamp and river forms, diving for submerged food.

Speciation

Where continental variation occurs it is of a clinal nature, vide *Podiceps novaehollandiae* (Mayr, 1943). Isolation and differentiation does, however, occur in this species beyond Australia.

Order FALCONES

Families ACCIPITRIDAE, FALCONIDAE, PANDIONIDAE

(Hawks and Eagles)

The Australian eagles and hawks number 24 species and constitute a most varied fauna. At the one extreme are small "hovering" kites and a kestrel, at the other the large eagle *Aquila* *audax* with wingspan of up to ten feet. The majority of the forms are endemics (4 genera, 15-16 of the species) that have diverged to a greater or lesser extent from counterparts in other areas of the world.

The various forms are specialized ecologically in various ways: as scavengers, rodent and insect feeders, hunters that catch birds in the air, and as fish-eaters. Many are nomads and their distribution depends on seasonal conditions and the whereabouts of prey.

All the Australian hawks are well differentiated species.

Speciation

Fifteen of the Australian Falcones either do not vary geographically, or have only insignificant clinal variation. This results largely from the mobility that goes with large size and the strongly developed nomadic tendencies of most species.

Of those that do vary geographically, one species *Falco berigora*, does so to a marked degree. It is improbable, however, that any of its forms are true isolates today (Condon, 1951a).

Distinctive southern and northern forms occur in four species with evidence in at least one (*Accipiter fasciatus*), and possibly others (*A. cirrhocephalus, Falco longipennis, Pandion haliaetus*), that this state of affairs has been built up by invasion of the continent from the north taking place in two waves. In *Accipiter fasciatus* these consecutive arrivals are now connected by a stepped cline (Condon and Amadon, 1954).

Aquila audax and possibly *Accipiter novaehollandiae*, show some evidence of interruption to gene flow across Bass Strait. The northwestern stock of *Aviceda subcristata* and the southwestern population of *Falco peregrinus*, each of which has differentiated to some extent, are apparently isolated.

Although there is evidence in a few species of minor isolation and range thinning, there would not appear to be any species being formed in the Australian hawks today. In the island section to the east of Wallace's Line, by contrast, the Australian species are broken up into about 43 morphologically differentiated isolates. This is exclusive of the variation occurring to the west of the Line in cosmopolitan, or Afro-Asian, species such as *Milvus migrans, Haliastur indus, Falco peregrinus,* and *Pandion haliaetus*.

Order GRESSORES

Families ARDEIDAE, THRESKIORNITHIDAE, CICONIIDAE

(Herons, Spoonbills, Ibises)

The 19 species that make up the Australian members of this order may be divided up as follows: — swamp bitterns, 2; mangrove bitterns, 1; egrets, 3; night herons, 1; stream and swamp herons, 4; reef herons, 1; estuarine herons, 1; spoonbills, 2; ibises, 3; storks, 1. All of these extend beyond Australia and a few belong to widespread superspecies. The majority of the forms are predominantly swamp feeders but the herons hunt in the open fields, fringes of streams, and tidal flats as well. One species is confined to mangroves and a second is exclusively a reef feeder.

The Australian Gressores almost all have a wide range on the continent and typically are nomads, moving around with seasonal conditions. Breeding areas vary somewhat from year to year, depending on water levels on individual marshes and streams (H. J. Frith, personal communication).

A couple of species, however, are seaside feeders, and exhibit little seasonal movement. These are the Mangrove Heron, *Butorides striata*, and the Reef Heron, *Demigretta sacra*.

Speciation

None of the members of this group vary geographically except (a) *Threskiornis molucca*, that apparently shows a slight south-north size cline, and (b) *Butorides striatus*, that has no fewer than five differentiated isolates (Mayr, 1943). Under circumstances of insular isolation in the southwest Pacific, by contrast, *Nycticorax caledonicus* has 2 distinctive isolates, *Dupetor flavicollis* at least 2, and *Butorides striatus* 4.

The Australian isolates of *B. striatus* occur as follows: (a) Shark Bay (unnamed form), (b) Ashburton River to Point Cloates (*rogersi*), (c) King Sound (*cinereus*), (d) Northern Territory and Melville Island (*stagnatilis*), (e) Cooktown area (*littleri*), and (f) New South Wales (*macrorhynchus*). These forms differ markedly in colour and size and one of them (*rogersi*) was long considered a distinct species. Mayr stresses the fact that the western and eastern groups are distinct, and suggests that they may have originated as a double invasion.

The pattern of isolation and differentiation in *B. striatus*, set out in Figure 8, is similar to that seen in some other mangrove birds (see Section IX).

Demigretta sacra has a similar distribution to *Butorides striatus* but does not vary geographically in Australia. It is a

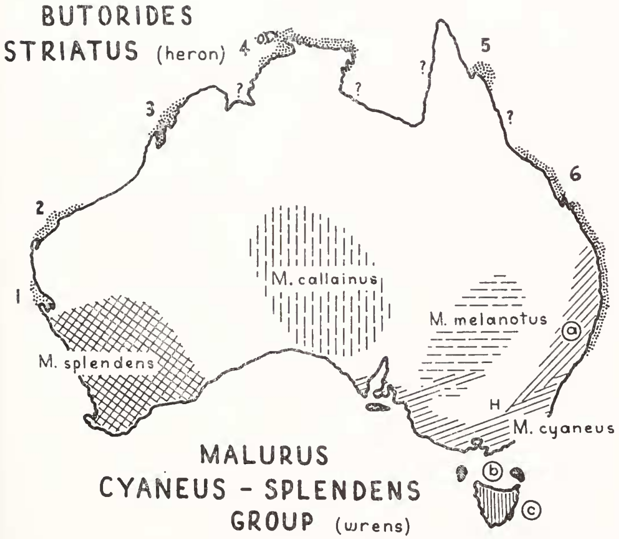

Fig. 8. *Upper:* Isolation and differentiation in the mangrove bittern (*Butorides striatus*). There is a chain of distinctive isolates along the western, northern, and eastern coasts (indicated by spotted areas and numbers). Range gaps correspond to areas where the appropriate habitat is apparently lacking.

Lower: Distribution of species and forms in the *Malurus cyaneus* — *melanotus* — *splendens* group of the blue wrens (see cross-hatched areas in lower half of map). The four major forms shown, though isolated from each other, are so distinct that (with the possible exception of *M. melanotus* and *M. callainus*) they must be regarded as (taxonomic) species. The habitats differ markedly, *M. cyaneus* inhabiting sclerophyll forest and thickets in savannah woodlands, *M. melanotus,* mallee, *M. callainus,* spinifex desert, and *M. splendens,* sclerophyll and dry scrubs.

M. cyaneus has isolated insular races on the Bass Strait islands and Tasmania. "H" refers to a minor zone of intergradation. The small letters, "a", "b", and "c" refer to races of *M. cyaneus.*

relatively "conservative" species, with only one morphologically differentiated isolate in the whole of the Pacific.

Order ANSERES
Family ANATIDAE
(Ducks)

There are 19 Australian species, many of them endemics. The fauna includes a number of curious monotypic genera such as the Black Swan (*Cheopis strata*), the Pied Goose (*Anseranas semipalmata*), the Cape Barren Goose (*Cereopsis novaehollandae*), the Pink-eared Duck (*Malacorhynchus membranaceus*), Freckled Duck (*Stictonetta naevosa*), and Musk Duck (*Biziura lobata*). By contrast, others are representatives of near cosmopolitan groups: teals, shovellers, and tree ducks.

The various members of the family are typically swamp and river forms, a few being animal feeders, but most are herbivorous or have a mixed diet. There are no true sea ducks in Australia.

Most species have a wide range. Some four are essentially southern, and three are confined to the tropical north. Only one species, *Cereopsis novaehollandiae*, has a really restricted range—the islands off the southern coast.

The most striking feature of the Australian Anatidae is the great mobility of most species. The Australian bird literature has many references to ducks arriving in various districts following heavy rain, remaining for a while and, with the drying up of the surface water, disappearing again. Recent banding work on one species, the teal *Anas gibberifrons*, has proven that individuals move seasonally between the north and south of the continent (e.g. Darwin — Perth, Darwin — southern New South Wales). The amplitude of movement of at least two other species (*Malacorhynchus membranaceus*, *Anas superciliosa*) is undoubtedly equally great.

The areas in which most duck species concentrate to breed vary somewhat from year to year but there is regular breeding both in southeast and southwest Australia (H. J. Frith, personal communication).

Speciation

The distinctive small teals, *Anas gibberifrons* and *A. castanea*, at one time considered to belong to the same species (Ripley, 1942) but now known to coexist over a wide area, represent the only case in which the circumstances of past speciation can be seen. The two apparently originated as a double invasion of the continent from the north, with *A. castanea* being the older inhabitant.

Geographic variation is negligible in the Australian Anatidae.

In contrast with the situation on the continent, a number of Australian ducks show well marked differentiation in the island archipelagos to the north. Thus, *Dendrocygna arcuata* has at least one morphologically differentiated isolate, *Anas superciliosa*, one, and *Anas gibberifrons*, one.

Order GALLI

Family RALLIDAE

(Rails and Water-hens)

Of the 14 species occurring in Australia, three extend through from the Palaearctic region (*Porzana pusilla, Fulica atra, Porphyrio porphyrio*). A few others belong to cosmopolitan superspecies (e.g. *Gallinula tenebrosa*). Two species have a wide range through the Pacific (*Hypotaenidia philippensis, Poliolimnas cinereus*). Of the remainder, three species occur also in New Guinea and adjacent islands and/or New Zealand (*Rallus pectoralis, Rallina tricolor, Porzana tabuensis*, plus *Porphyrio porphyrio* mentioned above). Four species are restricted to Australia (*Eulabeornis castaneoventris, Porzana fluminea, Amaurornis ruficrissus, Tribonyx ventralis*), and one (*Tribonyx mortieri*) to Tasmania.

With the exception of the northern *Rallina tricolor*, inhabiting undergrowth and thickets near tropical streams, and *Eulabeornis castaneoventris* and *Poliolimnas cinereus*, living in mangroves (also in the north), the Australian Rallidae are swamp and marsh species.

Speciation

Nine of the Australian Rallidae either do not vary geographically or have only minor clinal variation. Of these, four have a relatively restricted range (north of the continent or on Tasmania only). The others are either highly nomadic (e.g. *Fulica atra*), or at least nomadic over part of the range (*Tribonyx ventralis*).

The most marked isolation and differentiation occurs in *Porphyrio porphyrio*, the southwestern form of which (*bellus*) is highly distinct, the Tasmanian isolate (*fletcherae*) somewhat less so. *P. porphyrio* is a sedentary species. The southwestern populations of *Porzana fluminea, Gallinula tenebrosa* and *Rallus philippensis* are apparently isolates, as are the Tasmanian populations of *Rallus pectoralis* and *Porzana tabuensis.* The distinctive endemic rail of Tasmania, *Tribonyx mortieri,* may represent an early isolate of *T. ventralis*-type stock, though a fossil rail from southern Queensland (*T. effluxus* Devis (1892); see Condon, 1954, p. 23) could indicate that it is derived from a heavier-bodied stock now extinct on the mainland. *Eulabeornis castaneoventris* has a morphologically differentiated isolate in the Aru Islands

In contrast with the minor amount of isolation and speciation within Australia, several of the rail species have a large number of distinctive isolates beyond the continent. *Rallus philippensis* has a total of 18 differentiating isolates in the section to the east of Wallace's Line (including New Zealand, New Caledonia, and Macquarie Island — Peters, 1934, p. 164), *Porphyrio porphyrio* about 8 (in New Zealand, the Chathams, Lord Howe Island, various Pacific islands), whilst *Porzana tabuensis* has them in New Zealand, New Caledonia, Fiji, and elsewhere. The capacity of the short-winged rails for colonizing oceanic islands is well known. Here they typically occupy grass thickets and undergrowth, not marshes.

Order GRUES

Family TURNICIDAE

(Bustard-quails)

The Turnicinae and Pedionominae, respectively, contain six and one species. One member of the former extends to New Guinea and beyond, and another to New Caledonia.

All are swift-running, swift-flying, ground-living birds, partly seed-eating but also taking insects, and requiring long grass and herbage for protection. The various species are specialized for life on the open plain, rocky hillsides, swampy ground, forests and dense scrub.

The various species of *Turnix* vary in bill form, some having slim, others heavy graminivorous-type, beaks. This situation is reflected in *Amytornis.*

Speciation

Only two forms show any speciation trends in Australia: the stationary *Turnix varia* and *Turnix castanota*. The former, inhabiting sclerophyll forest (and mallee), is a coastal form of the east and south. It has isolates, none of them very well differentiated, in Tasmania, the southwest corner of the continent, and on the Abrolhos Islands. *Turnix castanota*, a savannah woodland inhabitant of the northwest of the continent, has a distinctive isolate (approaching the extent of differentiation typical of a species) on Cape York (*olivei*).

The remaining species either do not vary geographically or show only clinal variation. Most, however, are either nomadic (e.g. *T. velox*), or else have only a restricted range (*T. melanogaster*, *Pedionomus torquatus*).

There could be a degree of isolation, past or continuing, be tween the northwestern and eastern forms of *Turnix pyrrhothorax*.

Order COLUMBAE
Family COLUMBIDAE
(Pigeons and Doves)

The Australian pigeon and dove fauna totals 22 species, two-thirds of them endemic. *Chalcophaps indica chrysochlora*, however, is the end member of a chain of forms extending through from India and thence east to the New Hebrides. *Geopelia striata* extends from Malaya to Australia. *Ptilinopus regina* and *P.* (*cincta*) *alligator* stem from the islands to the northwest of the continent (e.g. Timor) and the parental stock of the endemic eastern *Macropygia phasianella* apparently also entered the continent from that sector (Mayr, 1944b). *Ptilinopus superbus*, *Megaloprepia magnifica*, and *Ducula spilorrhoa* are fairly recent immigrants from New Guinea, whilst the parental stock of the endemic *Columba norfolciensis* must have also entered from the northeast.

Within the Australian continent today the pigeon-dove fauna falls into a large number of morphologically and ecologically distinctive types. The fruit pigeons are as highly coloured as the interior ground dwellers are plain.

The various species may be grouped ecologically as follows:—

(a) *Rain forest forms.* Arboreal fruit and berry eaters, 8 species.

Forest floor species, 2 species.

(b) *Ground feeding form of the coastal undergrowth* (southern), 1 species.

(c) *Small arboreal doves* which feed on the ground and have a northern or inland range, 3 species.

(d) *Pigeons of the interior grasslands and desert* 5 species.

(e) *Rock Pigeons*, requiring rocky outcrops, 2 or 3 species.

The eastern rain forests have a dense fauna, as has the plains country of the inland. The rock pigeons inhabiting areas of rocky outcrops, are interior and northwestern in distribution.

Only two species occur in the southwest corner of the continent and in Tasmania (*Phaps elegans* and *P. chalcoptera*).

Speciation

The circumstances of origin of most endemic genera and species cannot now be seen. Some speciation is, however, occurring today.

The large rain forest fruit pigeon, *Megaloprepia magnifica*, has morphologically differentiated isolates corresponding to each of the three main tracts of rain forest: northern New South Wales-southern Queensland, Cairns-Atherton, and Cape York. Those inhabiting the last-named district are obviously recent arrivals from New Guinea. *Ptilinopus regina* and *Chalcophaps indica*, inhabiting monsoon forests and coastal scrubs in the Northern Territory and rain forests in the east, are differentiated into distinctive eastern and northwestern isolates. *Ptilinopus alligator*, known only from the Alligator River, is a distinctive derivative of the Timor-Sumba species, *Ptilinopus cincta*.

Amongst the savannah woodland-grassland species, *Geophaps scripta* and *G. smithii*, inhabiting Arnhem Land and Cape York-eastern Australia, respectively, have developed specific differences. The small doves, *Geopelia striata* and *G. humeralis*, and the crested pigeon, *Ocyphaps lophotes*, have undergone differentiation in the savannah tract in the Hamersley area of Western Australia. *G. striata* and *G. humeralis* have developed morphologically distinct isolates in the savannah area of southern New Guinea. *G. striata* has a hybrid zone in northwestern Australia.

The rock pigeons of central and northwestern Australia require a combination of rocky outcrops, spinifex, and surface water (Mayr, 1951) — an exceptional habitat. They are broken up into morphologically differentiated isolates to a surprising extent. *Lophophaps plumifera* has no fewer than 3-4 (see figure in Mayr, 1951), distributed as follows: (a) Midwestern Ausfera) (this form extends across the continent to western Queensdistrict, at mouth of the Fitzroy River (*mungi*); (c) West Kimberleys (middle Fitzroy and Margaret Rivers) (*proxima*); (d) Middle Victoria River and Eastern Kimberleys (*plumifera*) (this form extends across the continent to western Queensland); (e) Central Australia (*leucogaster*).

These forms are apparently isolated from each other, the barriers separating them (sand plains) being terrain deficient in the basic requirements.

The genus *Petrophassa* contains two distinctive forms, *albipennis* and *rufipennis*, respectively isolated in the rugged gorges of the Kimberleys and Alligator River section of Arnhem Land. They are approaching, or have reached, that degree of differentiation typical of species.

In contrast to the above cases, there are several Australian Columbae that either do not vary geographically or else have only minor size or colour clines. These include: (a) *Phaps elegans*, an inhabitant of the southern and southeastern coastal fringe that has undifferentiated isolated populations in Tasmania and southwestern Australia. The population of *Leucosarcia melanoleuca* isolated in the Cairns rain forest may also prove to be undifferentiated. (b) *P. chalcoptera*, a large pigeon with a continent-wide range and that is essentially sedentary (and hence might be expected to vary). (c) A couple of eastern rain forest nomads (e.g. *Columba norfolciensis*), a highly nomadic interior species (*Histriophaps histrionica*), and a nomadic inhabitant of the northern coastal fringe (*Ducula spilorrhoa*).

Species with morphologically differentiated isolates beyond Australia are: *Chalcophaps indica*, 4 (plus an additional 4 to the *west* of Wallace's Line); *Ptilinopus regina*, 2-3; *Megaloprepia magnifica*, 3; *Ducula spilorrhoa*, 1; *Geopelia striata*, 3.

Order PSITTACI
Family PSITTACIDAE
(Parrots)

The Australian parrot fauna numbers about 50 species and, with the exception of half a dozen species obviously of northern origin (e.g. *Trichoglossus moluccanus, Opopsitta diophthalma, Probosciger aterrimus, Larius roratus*), is completely endemic. Radiation has been marked in all the basic ecological types.

These include: (a) somewhat generalized seed-eaters, inhabiting the wide areas of the continent covered by grassland savannah, (b) large heavy-billed cockatoos, that either eat the larger seeds and nuts, dig for roots, or else strip the bark from trees in search of wood-boring grubs, and (c) small, nectar-feeding lorikeets that exploit the large blossoms of the dominant *Eucalyptus, Grevillea,* and *Banksia* trees.

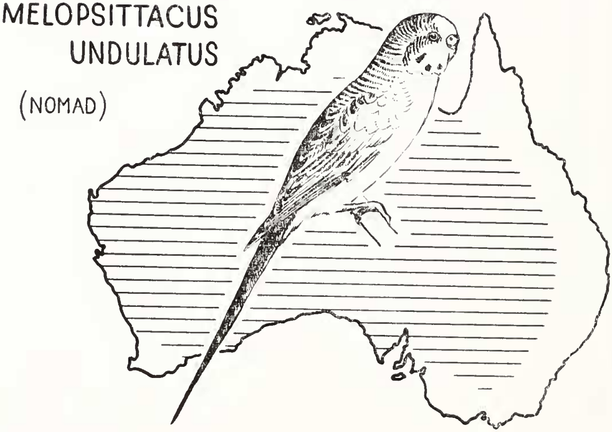

Fig. 9. The influence of nomadism on geographic variation. *Melopsittacus undulatus,* the domesticated budgerigah or "parrakeet," is typical of the many interior species that are highly nomadic and breed wherever conditions are propitious. In none of the species with this form of seasonal behaviour does geographic variation or speciation occur.

The family Psittacidae is represented by species in all the major vegetation formations excepting mangroves and swamps. The majority of species are sedentary but nomadism is well developed in some of the inland grass-feeders, e.g. *Leptolophus hollandicus* and *Melopsittacus undulatus* (Fig. 9), and in many of the nectar feeders (*Trichoglossus* and *Glossopsitta*) that seasonally follow the flowering of the trees.

Speciation in Some Major Genera

As the various genera present a complicated variety of speciation situations they can best be reviewed individually.

Opopsitta: O. diophthalma, a rain forest fig-feeder, has three distinctive isolates confined, respectively, to the three major tracts of rain forest occurring in Australia (Fig. 10). Those populations inhabiting the two more southern tracts (*coxeni*, *leadbeateri*) have obviously been isolated for a considerable period of time for they are approaching the degree of differentiation typical of species. That inhabiting Cape York (*marshalli*), however, is presumably a recent immigrant for it is only doubtfully distinguishable from that inhabiting the Aru Islands.

Platycercus: The various species fall into two superspecies: *elegans-flaveolus-caledonicus* (Fig. 11), and *eximius-icterotis-adscitus-venustus* (Fig. 12).

The *P. elegans* group is fundamentally an inhabitant of the eastern coastal rain forests and mountain sclerophyll forests. In the Murray basin, however, in association with the development of morphological differences, one stock (*flaveolus*) has secondarily become adapted to inland riverside savannahs. Members of the *P. eximius* group inhabit savannah woodland and sclerophyll forest. They have much the wider range, with southwestern and northwestern representatives.

In *P. elegans* there is a distinctive isolate in the Cairns rain forest (*nigrescens*), and a Tasmanian isolate that is so distinctive that it is regarded as a species (*P. caledonicus*). The form inhabiting Kangaroo Island, at the western extremity of range, is similar to that of Victoria, but extending inland from the adjacent mainland is a chain of distinctive forms in which the dominant red pigment is gradually replaced by yellow (Condon 1941; Cain 1955). The forms, former isolates (?), are apparently connected by hybrid zones today. The end member (*flaveolus*), the most distinct, extends practically the entire length of the Murray. Towards the headwaters, however, it makes contact with typical *P. elegans* without interbreeding (Fig. 11). The situation thus is one of speciation by circle formation, the individual links of which are interfertile but the end members are not.[1] This is the only case of this type in Australian birds (Cain, 1955).

In the *P. eximius* group, inhabiting savannah woodland and sclerophyll forest there are major forms in the southeast (*P.*

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[1] One hybrid bird has since been found in the overlap area.

eximius), southwest (*P. icterotis*), northeast (*P. adscitus*), and northwest (*P. venustus*) of the continent, respectively (Fig.

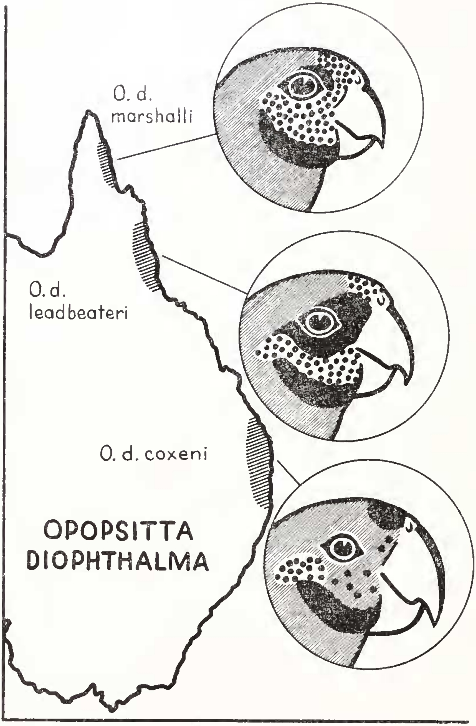

Fig. 10. Isolation and speciation in the rain forest fig-parrot, *Opopsitta diophthalma*. There is a distinctive form corresponding to each of the three major rain forest tracts in Australia.

Note differences in bill size and in the distribution of the red (spotted) and blue (black) areas on the head.

Rain forest species are often represented by distinctive forms in each of the three large tracts (New South Wales — southern Queensland, Cairns-Atherton and Cape York).

12). They obviously originated in these sections and from there spread out into the ranges they occupy today. Isolation remains complete in all instances except between *P. adscitus* and *P. eximius* where there is an area of overlap, in which some hybridization occurs. These major forms are so distinct morphologically that they can only be called species, although further study of the relationship of *P. eximius* and *P. adscitus* is required.

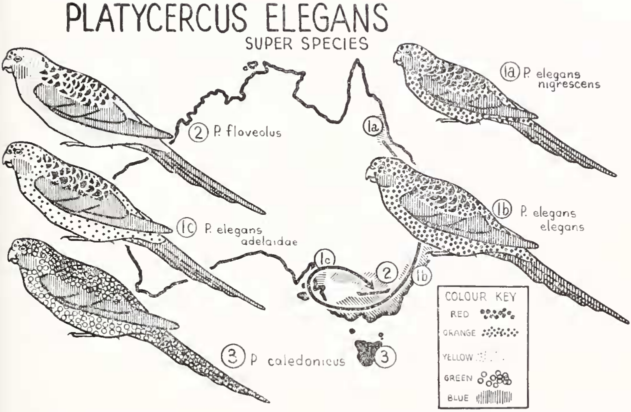

Fig. 11. Isolation and speciation by ''circle formation'' in rosella parrots of the *Platycercus elegans* superspecies. Distinctive isolates occur in the Cairns-Atherton rain forests (*elegans nigrescens*) and on Tasmania (*caledonicus*). These are indicated by ''1a'' and ''3'' on the map, respectively. *P. elegans* proper (1b) extends through the sclerophyll forests of the eastern coastal strip. In southeastern South Australia, however, it is genetically connected, through a chain of interfertile forms (e.g. *P. e. adelaidae*—''1c'') and hybrid zones, with *flaveolus* inhabiting the riverside savannahs of the Murray-Murrumbidgee River system (''2''). Towards the headwaters of these streams *flaveolus* and *elegans* make contact without interbreeding.

Within the four species, minor isolates occur on Tasmania (*P. eximius diemenensis*) and, currently or formerly, in various parts of coastal Queensland (e.g. Cape York, Cairns-Atherton area, Bowen area) in *P. adscitus*.

Barnardius: Speciation is also marked in this genus. As suggested by the map of Gentilli (1949), it is probable that *B. zonarius* originated in the southwest and *B. barnardi* in the east of the continent, respectively, at a time of greater aridity than today. Subsequently, *B. zonarius* has been able to extend to the east, crossing the Nullarbor Plain. Cain (1955) indicates that hybridization between the two occurs today in the vicinity of the Flinders Range.

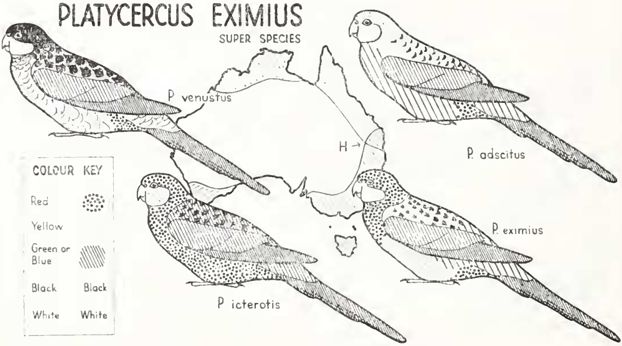

Fig. 12. Isolation and speciation in the *Platycercus eximius* group of savannah woodland — sclerophyll forest rosella parrots. Geographically-representative forms, so distinctive that they are called species, occur in the northwest, northeast, southeast, and southwest of the continent, respectively. Secondary range contact and some hybridization ("H") occur between *P. adscitus* and *P. eximius* today. The status of these forms requires further investigation.

P. eximius has a minor insular isolate on Tasmania.

The most interesting feature of *Barnardius* is that a series of distinctive isolates have developed in the various river systems in different parts of the continent. There are such forms centred on the group of rivers entering the head of the Gulf of Carpentaria in the north (*b. macgillivrayi*), the Hamersley (mid-western) watershed (*z. occidentalis*), the Murchison River (*z. connectens*), the southwest (*z. semitorquatus*), the streams arising in the Macdonells in central Australia (*z. myrtae*), and the Murray-Darling system (*b. barnardi*). The distribution of the group is essentially a ''refuge'' one.

Psephotus: This genus of 5 to 6 species falls into three species groups, representing earlier and later phases of radiation and speciation. These, and the vegetation formations they now occupy, are as follows: (a) *P. haematogaster* (with 5 subspecies, a couple of which are undoubtedly isolates), southern inland Australia (areas of savannah grassland, mallee, and mulga); (b) *P. haematonotus* (little geographic variation), inhabiting the temperate savannah woodland of southeastern Australia; (c) *P. varius* (savannah grassland and mulga), and the *P. chrysopterygius* superspecies (tropical savannah woodland mainly), including *P. c. chrysopterygius* on Cape York, *P. c. dissimilis* (Arnhem Land), and *P. pulcherrimus* (central and southern Queensland).

Speciation is actively occurring in the *P. varius-chrysopterygius* group, several isolates of which have reached the stage of morphological distinctness typical of species. The group has essentially a ''refuge-type'' distribution and the distribution of forms corresponds closely to that in the *Platycercus eximius* and other groups. These are: southeast of continent, in this case the Murray-Murrumbidgee system mainly (*P. varius orientalis*), southwest (*v. varius*), Arnhem Land (*chrysopterygius dissimilis*), Cape York (*c. chrysopterygius*), and eastern Queensland (*pulcherrimus*) — see distribution map in Cain (1955, Fig. 13). Of these *v. varius* has spread outward to central Australia and the Hamersleys.

Psephotus demonstrates a common phenomenon in Australian birds (*vide Climacteris, Platycerus*), namely, that where members of a genus live in close proximity to each other over an extensive area (including occupying adjacent habitats), they typically belong to *different* species groups. Alternatively, expressed, *within* each species group the members tend to be geographically representative, or else geographic overlap is only partial (more recent). The different rates at which differentiation and speciation may occur from one species group to another is also seen in *Psephotus,* in one group (*P. haematonotus*) there being no geographic variation, whereas in the others it is well advanced.

Neophema: Again there are three species groups, representing an earlier stage of radiation and speciation, plus a series of more recent forms. The species groups are: (a) *N. bourki* (inhabiting the arid interior, mainly mulga desert), (b) *N. chrysogaster — chrysostomus—elegans—petrophila* (southern riverside savannah woodland and dry sclerophyll forest, mostly), and (c) *N. pulchella-splendida* (southern dry sclerophyll-savannah woodland, and desert scrub, respectively).

It is within the second species group that much speciation has taken place. *N. chrysogaster* is fundamentally Tasmanian, though it now coexists with other members of the species on the mainland, and *N. elegans* probably originated in the southwest. It too occurs now in the southeast. *N. petrophila,* confined to the rocky coastline and offshore islands of the southwest and south, has the most unusual habitat and breeds in rocky crevices, not in trees. *N. chrysostoma* possibly originated in the interior (especially in the mallee areas) of the southeast. *N. pulchella* and *N. splendida*, making up the third group, isolated in the southeast and east and in the desert areas of southern Australia, respectively, also occupy dissimilar habitats.

Speciation in the Psittacidae, Summarized

Within the 32 members of this group covered, there are two instances of secondary range overlap by recently evolved species: the contact between *Neophema chrysostomus* and *N. elegans*, and the contact between the former and *N. chrysogaster* in southeastern Australia. In *Platycercus elegans-flaveolus* the end members of a chain of interfertile forms meet without interbreeding.

Isolates that have reached, or are approaching, that stage of morphological differentiation typical of genetic species occur as follows: *Opopsitta* (2), *Platycercus* (3), *Psophotus* (about 3), *Neophema* (about 2). There are some 13 morphologically differentiated isolates of lesser degree.

Hybrid zones occur between *Platycercus eximius* and *P. adscitus* and between *Barnardius zonarius* and *B. barnardi.*

The only parrots that do not vary at least somewhat geographically are nomads and those with restricted ranges. *Melopsittacus undulatus* and *Leptolophus hollandicus*, the first ranging widely over the continent (see Fig. 9), are examples of the former. Clines occur in continuously ranging species, e.g. *Kakatoe roseicapilla.*

Most species are confined to the continent and hence isolation and speciation is intra-continental. A couple of New Guinea species, however, have undifferentiated isolates on Cape York, e.g., *Larius roratus* and *Geoffroyus geoffroyi*. There is an interesting tendency in several parrot genera for river systems to act as refuges and for differentiation to occur within them.

Order CORACIAE
Families CORACIIDAE, ALCEDINIDAE, MEROPIDAE
(Rollers, Kingfishers, Bee-Eaters)

Only one roller (*Eurystomus*) and one bee-eater (*Merops*) occur in Australia, and both are south-north migrants, wintering in the islands to the north of the continent.

The Australian kingfishers number ten species and range from small four-inch long river kingfishers (*Alcyone*) to large forest kingfishers (*Dacelo*) a foot in length. The majority of species have had a northern origin but four are Australian.

Most are sedentary but south-north migration occurs in *Halcyon sancta, H. macleayi*, and *Tanysiptera sylvia*. The only true inland form, *H. pyrrhopygia*, is nomadic.

The various species fall into several well defined groups:— *Alcyone* (2 species), short-tailed diving forms; *Dacelo* (2) large forest forms and true endemics; *Halcyon-Syma* (5), forest and mangrove inhabitants, three of which are certainly recent immigrants with two (*H. chloris* and *H.* (*australasiae*) *sancta*) belonging to widely ranging Asio-Pacific species groups; *Tanysiptera* (1), long-tailed tropical kingfishers of New Guinea origin.

Speciation

Neither the roller, *Eurystomus orientalis*, nor the bee-eater (*Merops ornatus*) varies geographially in Australia.

Speciation in the kingfishers is limited to a series of isolates, as follows: (a) *Dacelo leachii*, inhabiting the northern savannah woodlands (isolates in the Gascoyne — De Grey segment of northwestern Australia), (b) *Syma torotoro* and *Tanysiptera sylvia*, restricted to Cape York, which populations are differentiated from the parental New Guinea species; (c) *Alcyone azurea* and *Halcyon macleayi*, river and savannah woodland species, respectively, differentiated into Arnhem Land and eastern forms. There is also a fair measure of isolation between the Australian and New Guinea forms in *Alcyone azurea*, *Halcyon macleayi*, and *Alcyone pusilla*. The small Cape York form (*minor*) of *Dacelo novaeguineae*, an eastern and southern sclerophyll forest-savannah woodland species, almost certainly developed in isolation. The Tasmanian and Mount Lofty populations of *Alcyone azurea* are undifferentiated isolates.

A hybrid zone occurs in *Alcyone pusilla* in the Gulf of Carpentaria-Cape York area.

Size and colour clines occur in several species. In *Dacelo leachii* the Torres Strait barrier has led to a reversal of the species south-north size cline, the New Guinea population having a longer wing than the one on the adjacent mainland.

The nomad *Halcyon pyrrhopygia* and the migrant *H. sancta* have only negligible variation in Australia.

Beyond Australia, *Halcyon chloris* has some 40 morphologically differentiated isolates in a range from Africa to Polynesia. *H. australasiae*, of which *H. sancta* is a derivative, has a dozen or more. *Alcyone* and *Syma* have various forms in New Guinea.

Order PASSERES

Families MENURIDAE AND ATRICHORNITHIDAE

(Lyrebirds and Scrub-birds)

The lyrebirds (*Menura*), large, ground-living, long-tailed forest inhabitants fall into two species, one inhabiting the Macpherson Range, and the other the coastal forests of the east and southeast. The equally unique scrub-birds (*Atrichornis*), requiring dense undergrowth, are confined to eastern Australia (*A. rufescens*) and southwestern Australia (*A. clamosus*) — see map in Chisholm (1951).

All members of the group are sedentary species.

Speciation

Atrichornis falls into the common pattern of an evolving group being severed into an eastern and a southwestern component, the latter, *A. clamosus*, which has become extinct since settlement, being very distinct.

Menura alberti, the only bird species to be confined to the Macpherson Range rain forests, probably originated there for the area is obviously a refuge of long standing. *M. novaehollandiae* has presumably secondarily spread from the south, for it now reaches southern Queensland. It has, moreover, given rise to a distinct (? isolated) form (*edwardi*) in the Stanthorpe granite belt.

Family CAMPEPHAGIDAE
(Cuckoo-Shrikes)

The eight species that constitute the Australian Campephagidae include both older endemic forms and recent colonizers. The most interesting of the former is *Pteropodocys maxima,* a ground-feeding species of the dry interior, which is partly nomadic. Most species, by contrast, occupy a somewhat generalized food niche — the larger insects of the branches and foliage.

The endemic *Coracina robusta* of southern Australia and its "advanced" northern counterpart (*C. papuensis*), that lacks the immature plumage phase, obviously represent two distinct invasions from the north. *C. novaehollandiae,* the Australian populations of which are the end members of a chain of forms extending from India through Indonesia, has had a long period in Australia for it is broken up into several distinct forms here and has secondarily colonized New Caledonia to give rise to a new species there, *C. caledonica. Lalage sueurii* possibly originated in Australia for the endemic race (*tricolor*) is unique in having an eclipse plumage (Mayr, 1940b) and is well adapted to the dryer parts of the continent.

The remaining cuckoo-shrikes (*Coracina lineata, C. tenuirostris,* and *Lalage leucomela*) are fairly recent colonizers of the Australian continent from the north.

Speciation

Morphologically differentiated isolates occur in the Australian Campephagidae, as follows: *Coracina novaehollandiae,* inhabiting sclerophyll forest and savannah, 2, possibly 3 (one well differentiated); *C. papuensis,* tropical savannah woodlands, 2, possibly 3, all minor forms; *C. tenuirostris,* sclerophyll and savannah woodlands, 1 (probably), a minor form; and *Lalage leucomela,* rain forest fringes and mangroves, 2 or 3. The total of 7-10 continental isolates contrasts with 35 in those species (*C. papuensis, C. lineata, C. tenuirostris,* and *L. leucomela*) inhabiting an archipelago area in the southwest Pacific of equivalent size, and 48-49 for the whole island area east of Wallace's Line.

The ecological characteristics of this family relative to their tendency to undergo isolation and differentiation, have previously been discussed (Keast, 1958 i). Geographic variation tends to be absent or negligible in species occupying habitats that are broad as well as long (i.e. of an "inland" type), and that are continuous. It is suppressed in interior nomadic species, of which *Lalage tricolor* and *Pteropodocys maxima* are the main examples. South-north migrants, however, may vary geographically and even have isolates, e.g. *Coracina novachollandiae* and *C. tenuirostris.*

Clines occur in various species. *C. novachollandiae* has, in addition to a south-north cline of decreasing wing length, one of increasing bill length.

Family MUSCICAPIDAE
Subfamily MUSCICAPINAE
(Flycatchers, Fantails, and Whistlers)

This subfamily is made up of a mixture of Australian and New Guinea elements. Thus, of the four species of *Rhipidura*, *leucophrys* and possibly *fuliginosa* are Australian, and the other two are of tropical origin. The monotypic genus *Scisura* is Australian, whilst *Piezorhynchus, Machaerirhynchus, Arses, Monarcha, Heteromyias*, and *Tregellasia*, obviously originated in New Guinea or the adjacent islands. *Myiagra, Microeca*, and *Pachycephala*, are well developed both in the tropics and in Australia. The robin-like flycatchers (*Petroica, Eopsaltria*) are, by contrast, Australian, as are *Falcunculus* and *Oreoica* in the *Pachycephalini.*

The flycatchers are forest dwellers, with rain forest and sclerophyll forest being richest in number of species. A few are south-north migrants. The movements are partial (restricted to some populations) in *Rhipidura rufifrons, Myiagra rubecula, Monarcha melanopsis,* and *Pachycephala rufiventris,* and more general in *Petroica rodinogaster* (from Tasmania) and *Myiagra cyanoleuca.*

Speciation

The various flycatcher species differ widely in the extent and significance of their geographic variation. There are some three cases of recently completed speciation, various well differentiated isolates, a variety of minor isolates, and a couple of minor hybrid zones. Several species have striking colour and size clines. Others, however, do not vary at all geographically.

(a) Instances of Recently Completed Speciation

Petroica rodinogaster: This species is an insular (Tasmanian) derivative of *P. rosea*. *P. rodinogaster*, however, now migrates across Bass Strait to winter, and sometimes breeds, alongside the Dandenong Range population of its parent. The two behave to one another as good species.

Petroica vittata: This is an insular (Tasmanian) isolate of *P. cucullata* that, in dropping the pied male plumage of its parent form and reverting to a brown "henny" plumage, has

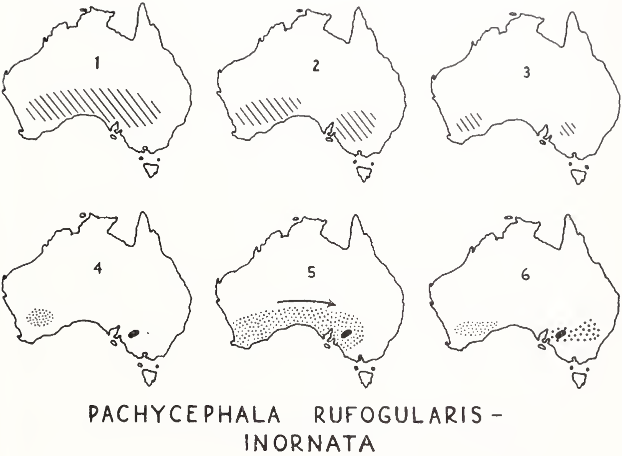

Fig. 13. Speciation in the *Pachycephala inornata* — *P. rufogularis* group of mallee thickheads, a suggested hypothesis.

The distribution of species and races today are as shown in the final map with *P. rufogularis* (see black ellipse) being confined to a restricted section in western Victoria. *P. inornata* is isolated into western (*inornata inornata*) and eastern (*gilberti*) races, indicated by light and heavy stippling, respectively.

It would seem likely that a widely ranging parental form (map 1) became split and isolated in the western and eastern sections of the continent, respectively (maps 2 and 3), there to build up genetic differences (map 4). Subsequently, *P. inornata* colonized eastwards, to co-exist with P. *rufogularis*. More recently, in accordance with the severence of the mallee habitat, the former has become broken up into eastern and western isolates.

The hypothesis presupposes south-north shifts of the rainfall belts causing vegetational changes.

undergone marked differentiation. It remains isolated, however, though specific distinctness can certainly be assumed.

Eopsaltria georgiana and *E. australis* (race *griscogularis*): This is a case of speciation by double invasion into the forested corner of southwestern Australia, the former being the older stock.

Pachycephala rufogularis: This species occupies a very restricted range in the Victorian mallee, where it coexists with the eastern form of its near relative, *P. inornata.* There would seem to be little doubt that the two developed in the eastern and western mallee tracts, respectively, when the parental stock became severed into two (Fig. 13). *P. inornata* was subsequently able to extend eastwards again to coexist with, and spread much wider than the essentially relict *P. rufofularis.*

(b) Morphologically Differentiated Isolates

Isolates so distinctive that they must be considered to be approaching the degree of differentiation typical of species are:

(i) The Arnhem Land and Cape York populations of the monsoon forest robins, *Poecilodryas superciliosa* (*cerviniventris* and *superciliosa*).

(ii) The southwestern and southeastern populations of the sclerophyll savannah woodland robin, *Eopsaltria australis* (*griscogularis* and *australis*).

(iii) The northwestern and northeastern forms of the mangrove whistler, *Pachycephalia simplex* (*simplex* and *peninsulae*).

(iv) The northwestern, southeastern, and southwestern forms of the sclerophyll-savannah woodland shrike-tit, *Falcunculus frontatus* (*whitei, frontatus, leucogaster*).

The total number of morphologically differentiated isolates in the Muscicapinae will be seen from Table 5 to be 31-35. They occur in the following species, whose habitat is also given:

Rhipidura fuliginosa, various habitats, 4-5, one of which is well differentiated; *R. rufifrons,* rain forest, 1, well differentiated; *Seisura inquieta,* savannah woodland, 2, one major, one minor; *Piezorhynchus alecto,* mangroves and rain forest, 2, one major, one minor; *Myiagra rubecula,* sclerophyll forest, 1, minor; *Machaerirhynchus flaviventer,* rain forest, 1, minor; *Monarcha trivirgata,* rain forest, 1, major; *Microeca leucophaea,* savannah and sclerophyll, and *M. flavigaster,* tropical savannah woodland, 1 each, both minor; *Petroica multicolor,* sclerophyll forest, 1, minor; *Eopsaltria australis,* sclerophyll forest and savannah, 2, one major, one minor; *Poecilodryas superciliosa,* monsoon forest, 1, major form; *Tregellasia capito,* rain forest, 1, minor; *Pachycephala pectoralis,* various habitats, 5-7, minor and major forms; *P. inornata,* mallee, 1, a minor form; *P. lanioides,* mangroves, 3, minor forms; *P. simplex,* mangroves, 1, major form; and *Falcunculus frontatus,* sclerophyll and savannah woodland, 2, major forms.

In addition to the above there are several cases of isolation without differentiation in the Muscicapinae, e.g. *Petroica chrysoptera* and *P. multicolor* in Tasmania.

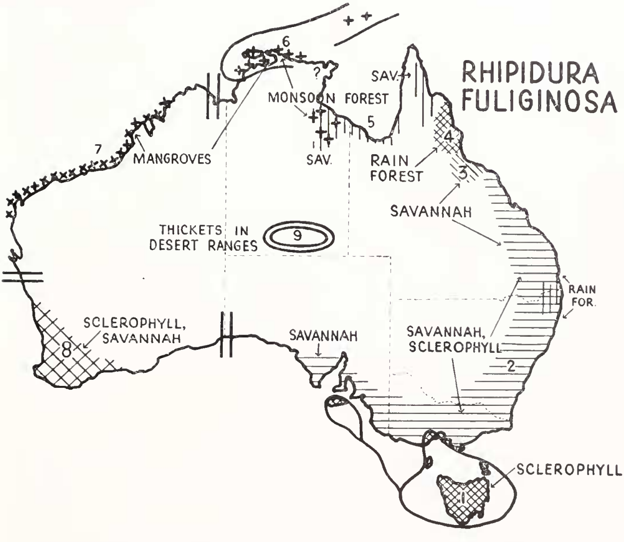

Fig. 14. Geographic variation in habitat preference in the long tailed flycatcher *Rhipidura fuliginosa.* This species, with essentially a peripheral range, occupies different habitats in various parts of the continent. This form of ecological variation indicates how, simultaneously with the development of genetic and morphological characters, isolates can become specialized for life in vegetation formations different from that occupied by the parental form.

The numbers 1-9 on the map indicate races and isolates. The pairs of parallel lines represent distributional barriers (see Keast, 1958a).

Note the isolate (9) in the mountains of central Australia.

Rhipidura fuliginosa (Fig. 14) and *Pachycephala pectoralis* provide interesting examples of geographic variation in the vegetation formation occupied, coincident with the acquisition of geographic morphological differences. In different parts of the range they inhabit rain forest, sclerophyll forest, savannah woodland, mangroves (and in the case of the latter even mallee) — see Section XII.

Colonization by New Guinea rainforest species across Torres Strait has been the main way in which new flycatchers have been added to the Australian avifauna, the group being best developed in the tropics. Various stages of differentiation from parental New Guinea stocks occur in Cape York in the different species.

Three recent colonizers, confined to the northern tip of the Peninsula, have yet to differentiate: *Monarcha frater, Microeca griseoceps* and *Tregellasia leucops.* In *Monarcha trivirgata,* an immigrant New Guinea stock (*albiventris*) occupies the northern part of this peninsula and a well-differentiated Australian form (*gouldi*) the southern part. They possibly meet and hybridize. In *Machaerirhynchus flaviventer,* the descendents of an earlier wave of colonization are now isolated in the Cairns-Atherton rain forests (*secundus*) and the later ones on northern Cape York (*flaviventer*). In the genus *Arses* there is a similar situation but in this case the earlier form is now so distinctive that, though still isolated, it must be regarded as having reached species status (*A. kaupi*). The later invader, *A. telescopthalmus,* has itself now differentiated from the parental New Guinea stock (race *lorealis*).

There has been some reverse colonization of the savannah woodland areas of southern New Guinea by Australian species, the following having given rise to distinct isolates there: *Rhipidura leucophrys* (race *melaleuca*), and *Microeca leucophaea* (*zimmeri*).

Hybrid zones do not occur in the flycatchers except for some minor ones in *Pachycephala pectoralis* (Mayr, 1954a).

There are no nomadic species amongst the Australian flycatchers. Four species, however, have migratory populations in the southeast part of their range. This partial migration has not prohibited the development of geographic variation in these species, two of them having morphologically differentiated isolates (*Rhipidura rufifrons* and *Myiagra rubecula*), and two varying clinally (*Pachycephala rufiventris* and *Monarcha melanopsis*).

Size and colour clines are developed in most sedentary Australian flycatchers that have, on the one hand, an extensive

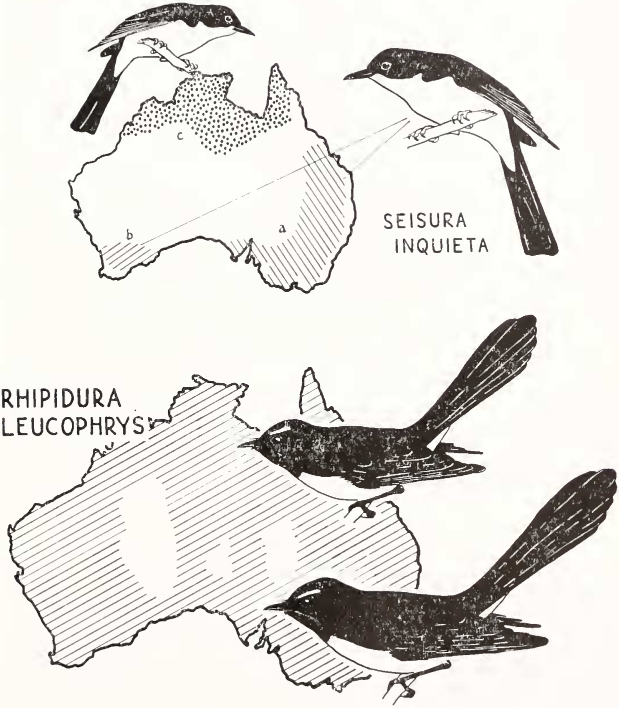

Fig. 15. The influence of isolation on south-north clines of decreasing size. Bergmann's Rule has a wide application in Australian birds. In the continuously ranging *Rhipidura leucophrys* southernmost and northernmost populations differ in size by 11 per cent.

In *Seisura inquieta,* however, in which there is a gap in the range, the difference is 22 per cent (see Keast, 1958a).

The letters a, b, and c indicate isolated populations of *S. inquieta.*

south-north range and, on the other, range through areas of widely differing rainfall. Thus, size clines occur in *Rhipidura leucophrys*, *Petroica cucullata*, and *Myiagra rubecula*. *Seisura inquieta* (Fig. 15) provides an interesting demonstration of the effects of isolation on a south-north size cline. Southernmost and northernmost populations in this species differ in size by about 22 per cent, the range gap being in northeastern Queensland. In the comparable *Rhipidura leucophrys*, in which the range is continuous, it amounts to only 11 per cent.

Speciation and radiation in the islands of the southwest Pacific are taking place in three "Australian" flycatcher species (Table 5). These are: *Rhipidura rufifrons* (Mayr and Moynihan, 1946), which has some 20 morphologically differentiated isolates, *Petroica multicolor* (Mayr, 1934), with about 12, and *Pachycephala pectoralis* (Galbraith, 1956) with over 50. The last-named is the richest of all bird species in number of races (Mayr, 1954a, p. 11). In addition to the above, the genus *Petroica* has given rise to many island forms in the New Zealand area (Fleming, 1950).

Subfamily TIMALIINAE
(Babblers)

The seven members of the Tribe Cinclosomatini covered in the present review are all inhabitants of the heavily forested regions except for the arid-country *Sphenostoma cristatum* and the mallee species *Drymodes brunniopygia*.

Speciation

Psophodes is composed of two species, one (*P. olivaceus*) restricted to the rain forest and sclerophyll forest regions of the eastern seaboard and the other the "ecologically-versatile" (*P. nigrogularis*) inhabitating the sclerophyll and mallee of the southwest, with an isolated relict race in the eastern mallee tract (*leucogaster*). Keast (1958g, Figs. 1 and 2) has suggested a series of steps, associated with major climatic oscillations, reflected also in *Pachycephala inornata-rufogularis*, to explain speciation in the genus. These are: (a) a parental stock formerly ranging right along the southern seaboard; (b) isolation of the stock into eastern and western populations as the result of climatic deterioration, and/or edaphic changes; (c) ecological and morphological modification of the western population, the result of its being more exposed to the harsh environment; (d) eastward colonization of the western mallee-adapted form, now specifically distinct (*P. nigrogularis*); (e) isolation of *P. nigrogularis* into eastern and western forms as a result of the mallee becoming divided into two tracts.

Psophodes is interesting in that it demonstrates a pathway of adaptation from life in the luxurious coastal forests to that in the semi-arid mallee. There is evidence that the southwest has also given rise to dry-country forms in other bird groups.

The genus *Drymodes* has a surprising distribution, one species inhabiting the southern mallee and the second (basically a New Guinea one) the rain forests of Cape York. The latter has, moreover, a minor isolate some 400 miles to the west on the Roper River (*colcloughi*), the only bird species to have an outlyer confined to this section. The origin of this race, like the circumstances of the original isolation of the species themselves, is obscure.

Orthonyx is composed of two species, *O. temminckii* and *O. spaldingii.* The former has a surprising pattern of distribution, the rain forests of eastern Australia from the Illawarra district, New South Wales, to the Bunya Mountains, Queensland (with minor range gaps) and then reappearing, as a distinctive colour form, 1500 miles to the north in New Guinea. *O. spaldingii* is confined to the Cairns-Atherton rain forest tract.

The monotoypic *Sphenostoma cristatum* shows only clinal variation.

Subfamily SILVIINAE
(Old World Warblers)

The only Australian representatives of this Palaearctic subfamily (Mayr and Amadon, 1951) are *Megalurus* (2 species), *Acrocephalus* (1), and *Cisticola* (2). *Acrocephalus* and *Cisticola* are Ethiopio-Palearctic genera.

Speciation

The swamp-dwelling *Megalurus gramineus* has minor isolates in Tasmania and in the southwestern corner of Western Australia, but *M. timoriensis,* despite an extensive peripheral range, does not vary geographically in Australia (Keast, 1956b).

Acrocephalus arundinaceus has distinct western and eastern forms, whilst there is also possibly an isolate in the Kimberleys (Mayr, 1948). *Cisticola* is represented by two species, both of which have a wide extra-Australian range and are only secondarily Australian. One of these, *C. exilis*, has some four colour forms within the continent and possibly fairly complete isolation as between the populations inhabiting the east and northwest of the ranges (Lynes, 1930; Keast, unpublished). The other, *C. juncidis*, has isolated, differentiated populations in the Normanton and Darwin areas respectively.

Subfamily MALURINAE
(Australian Warblers)

In contrast with the Muscicapinae almost all the members of the Malurinae occurring in Australia originated within the confines of the continent. Those genera that are restricted to Australia are *Epthianura*, with its monotypic derivative *Ashbyia* (5 species), *Acanthiza* (10 species, plus one in the mountains of New Guinea), *Amytornis* (7 species), *Malurus* (7 species, plus one in New Guinea), *Smicrornis* (monotypic), *Aphelocephala* (3 species), *Pyrrholaemus* (monotypic) *Hylacola* (2 species), *Calamanthus* (2 species), *Cthonicola* (monotypic), *Origma* (monotypic), *Pycnoptilus* (monotypic), *Cinclorhamphus* (2 species), *Daspornis* (2 species), *Stipiturus* (2 species), *Acanthornis* and *Oreoscopus*, the last two monotypic derivatives of *Sericornis*.

Gerygone (9 Australian species) and *Sericornis* (5 species) are equally developed in New Guinea and Australia. The island, for its part, has several endemic genera that are close relatives of those occurring in Australia (e.g., *Todopsis*).

The Australian warblers are all small, basically insectivorous, species. They inhabit either the foliage or ground and low undergrowth, with most genera being specialized toward one or the other zone. *Acanthiza* and *Sericornis*, however, have representatives in both zones. Those that live in the undergrowth are mostly characterized by long upturned tails, e.g. *Malurus*, *Amytornis*, *Stipiturus* and, to a lesser extent, *Hylacola*. The Australian Malurinae total 62 species.

Speciation in the Major Genera

A number of the Australian "sylviid" genera provide excellent demonstrations of speciation within the confines of the continent. They can best be considered individually.

Fig. 16. Distinctive relict races of the chat, *Epthianura crocea* (numbers 1-4 and spotted areas on map) are isolated in river valleys 800-900 miles apart. Distribution of this species, requiring dense ground cover and submarshy conditions, can only be explained by the north of the continent formerly having been wetter and providing continuous, or near-continuous, habitat of the right type.

The black ellipse indicates the range of *Ashbyia lovensis,* an inhabitant of the gibber deserts. Though fairly sedentary, its range is continuous and restricted. It does not vary geographically.

Epthianura albifrons (see cross-hatched areas) is somewhat nomadic on the mainland (see A) and does not vary geographically. Interruption to gene flow by Bass Strait, however, has led to the development of a minor insular isolate on Tasmania (B).

Epthianura and *Ashbyia:* This group, reviewed in detail elsewhere (Keast, 1958c), demonstrates the close link between the type of seasonal movements undertaken by species and their tendency to develop morphologically differentiated isolates. Of the five species, *Epthianura crocea* is unique in being sedentary, widely ranging, and in having highly specialized habitat requirements. It has four isolated and well differentiated populations in river valleys, respectively 600, 700, and 800 miles apart in the north of the continent. *E. albifrons*, somewhat nomadic and with a coastal and inland distribution varies only in the insular Tasmanian population. *E. aurifrons,* habitat generalized, distribution interior (i.e., wide and continuous), nomadic but movements varying with area and seasonal conditions, has no geographic variation. *E. tricolor* has a generalized habitat and a continuous interior distribution. It is markedly nomadic and with a seasonal shift in abundance from south to north of continent. Breeding habits must accelerate gene flow. There is no regular breeding area but it breeds wherever conditions happen to be suitable. It may breed in autumn in centre and north of continent as well as in spring in south and it is a colonial nesting species. No geographic variation occurs. *Ashbyia lovensis* is restricted to arid gibber desert in centre of continent, a continuous but moderately restricted habitat. It is fairly sedentary. There is no geographic variation.

The number of morphologically differentiated isolates in the Australian chats is thus four. Three of these are in *Epthianura crocea* (Fig. 16).

Gerygone: Nine of the 15 species in this genus occur in Australia and they fall into perhaps 5 species groups. Three of these (*G. palpebrosa, G. magnirostris,* and *G. chloronota*) are of New Guinea origin. Within Australia the various species are adapted to habitats ranging from tropical rain forest to coastal woodlands, mangroves, and the arid interior. They are typically sedentary forms but two species, *Gerygone olivacea* and *G. fusca,* have (south-north) migratory races.

Speciation is actively occurring in the genus. *G. olivacea,* a sclerophyll forest-savannah woodland species, has isolates in north Queensland (a minor form), the northwest (*rogersi*), and southern New Guinea (*cinerascens*). The New Guinea *G. hypoxantha,* known only from Geelvink Bay, could be an early isolate of this species. The rain forest species *G. palpebrosa* is broken up into three fairly distinctive stocks, inhabiting the tracts of this association on Cape York (*palpebrosa*), Cairns-Atherton (*johnstoni*), and Mackay-Rockhampton (*flavida*). A second rain forest species, *G.* (*igata*) *richmondi* has isolated stocks (minor races) in eastern New South Wales-southern Queensland (*richmondi*), the Bowen-Mackay area (*amalia*), and Cairns-Atherton area (*monki*). The mangrove species, *G. laevigaster*, inhabiting the northern coastline from Derby to Normanton, is broken up into three minor forms inhabiting, respectively, the mangrove tracts in the following areas: Derby-Napier Broome Bay (*broomei*), Port Essington-Melville Island (*laevigaster*), and the Roper River-Norman River (*mastersi*). *G. cantator* of eastern Australia, a form approaching the degree of differentiation typical of a species, is apparently also a derivative of this stock. The distinctive infraspecific form *tenebrosa*, ranging from Carnarvon to King Sound, bears a similar relationship to the widely-ranging *G. magnirostris* (Meise, 1931).

G. c. chloronota of Arnhem Land is an Australian isolate of a New Guinea species.

There are thus some 10 morphologically differentiated isolates in the genus *Gerygone* within continental Australia.

A further interesting feature is that several of the "brown" species of *Gerygone* are relatively better differentiated on the basis of habitat and call notes than they are morphologically. This particularly applies to *G. richmondi*, *G. fusca*, and *G. laevigaster*.

Insular forms of *Gerygone* occur in New Zealand and on Lord Howe Island (*G. igata*).

Smicrornis: This monotypic genus lacks isolates but shows marked geographic colour variation, plus a minor south-north size cline. The occurrence of the colour forms in this species in broad belts from east to west across the continent shows an interesting correlation with rainfall and temperature. It has been suggested that specific climatic thresholds may operate to produce this rather interesting variation of the Gloger Effect (Keast, 1958h).

Aphelocephala: The three species in this genus are, respectively, inhabitants of arid gibber desert (*A. pectoralis* and *A. nigrocincta*) and savannah woodland-grassland (*A. leucopsis*). The gibber deserts, occurring mainly in two extensive south-north tracts, break up the savannah into eastern, central, and western sections, leading to minor isolates in the latter species. The others do not vary geographically.

Acanthiza: The thornbills extend widely over the continent. As many as five species may co-exist in an area (e.g., about

Sydney) but are nevertheless well differentiated ecologically, particularly in feeding zone and/or the sub-association occupied.

Acanthiza presents various interesting situations from the speciation viewpoint (Mayr and Serventy, 1938). There is a case of speciation by double invasion, *A. ewingi* and *A. pusilla diemenensis* representing successive waves of colonization of Tasmania. Well differentiated isolates that could be said to be approaching species status include *A. pusilla katherina* and *A. reguloides squamata* in northeastern Queensland.

The total number of morphologically differentiated isolates in *Acanthiza* (Table 3) is about 15, most of them minor forms.

In the sclerophyll and savannah woodland species isolates occur in: the Cairns-Atherton area (*A. pusilla katherina, A. nana flava*); central Queensland (*A. reguloides squamata*); Tasmania (*A. pusilla diemenensis, A. ewingi*); Mount Lofty area of South Australia (*A. reguloides australis, A. nana lactior, A. lineata clelandi*). There is a form of *A. pusilla* confined to Kangaroo Island (*zietzi*), and the population of *A. lineata* there (*chandleri*) agrees in colouration with that inhabiting Victoria, not the adjacent areas of South Australia. In addition to the above, *A. chrysorrhoa* has a well differentiated isolate in the region of the Gulf of Carpentaria (*normantoni*).

The distinctive colour types of *A. pusilla* and *A. chrysorrhoa* inhabiting southwestern Australia are of uncertain origin. They could represent western outlyers of forest stocks from eastern Australia, or be derived by local selection (the area is one of high rainfall) from adjacent dry country stocks (Mayr and Serventy, 1938; Serventy, 1953). However, the southwestern type of *A. pusilla* has secondarily extended right across the continent to New South Wales. In this section, accordingly, the coastal and interior races are quite distinct.

The interesting relict isolates of the ground-dwelling Samphire Thornbill (*A. iredalei*) inhabiting, respectively, the arid interior (*iredalei*), heath country in eastern South Australia (*hedleyi*), and samphire adjacent to St. Vincent's Gulf (*rosinae*), have been discussed by Condon (1954).

Attention is drawn by Mayr and Serventy (1938) to two noteworthy characteristics of the species *A. pusilla* and *A. chrysorrhoa*. They are particularly versatile ecologically, habitats being occupied that range from rain forest fringes with an annual rainfall of over 100 inches per annum, to savannah woodland, mallee, and mulga, in the 10-inch rainfall zone. Each is split up into a chain of wet, intermediate, and dry country races.

Sericornis: The rain forest-sclerophyll-savannah woodland superspecies *S. frontalis* is divisible into four basic forms which, in that they are largely isolated, may or may not be entitled to species status (Mayr, 1937). They inhabit the southwest (*S. maculatus*) and southeast (*S. frontalis*) of the continent, Tasmania (*S. humilis*), and Cape York — New Guinea (*S. beccarii*), respectively. *S. frontalis* and *S. maculatus* have given rise to a few hybrid individuals in South Australia (Mayr). *S. maculatus,* which occupies the dryer southwestern part of the continent, is broken up into 3-4 minor isolated forms, two of which occupy the Abrolhos and Recherche Island groups, respectively (Mayr and Wolk, 1953).

The rain forest species *S. citreogularis* and *S. magnirostris*, ranging from New South Wales to the Cairns-Atherton region, each have a minor isolate at the northern end of the range.

Hylacola: This genus contains two species so similar that they would be regarded as geographic races did they not occupy adjacent habitats in one restricted area. Of the two, *H. pyrrhopygia* is an inhabitant of heathy under-scrub within the sclerophyll formations of eastern and southeastern Australia. The other occupies this type of habitat in southwestern and South Australia, but in the eastern part of the range inhabits mallee. The contact zone, in the Bendigo area of Victoria, is where the two kinds of habitat come together.

Calamanthus: This genus is broken up into two stocks, a coastal one (*C. fuliginosus*) and an interior one (*C. campestris*), which differ significantly in size and colour. The two are largely isolated but intergrade in the Eyre Peninsula and Coorong section of South Australia, *C. campestris* moving down dry corridors into the coastal habitat of *C. fuliginosus*. The latter has minor isolates on Tasmania and in southwestern Australia.

Amytornis: This distinctive genus constitutes one of the few true desert groups in the Australian avifauna, the various species being basically inhabitants of *Triodia* (porcupine grass). Their habit is secretive and they keep low down. Dense continuous cover is the prime requisite. Distribution tends to be broken up into "pockets." Dispersive capacities are poor.

There are two species groups: *A. textilis* and *A. striatus*.

The genus is remarkable (Keast, 1958b) for: (a) Bizarre changes in bill-form, from that typical of an insect-eater to the heavy "seed-grinding," finch-like type occurring in the *A. textilis* group (Fig. 17). The degree of size and colour variation as between species in the *A. striatus* group (Fig. 18), is also exceptional. The two species groups exhibit evolutionary changes reminiscent of those seen in the Galapagos and Hawaiian archipelagos. (b) There are no fewer than 4 isolated populations, so distinctive morphologically that they must be genetic species, yet each known from only a single locality: *A. goyderi* (lower Macumba River, north of Lake Eyre), *A. dorotheae* (MacArthur River, Gulf of Carpentaria), *A. woodwardi* (Alligator River, Arnhem Land), *A. housei* (Charnley River, in the Kimberleys).

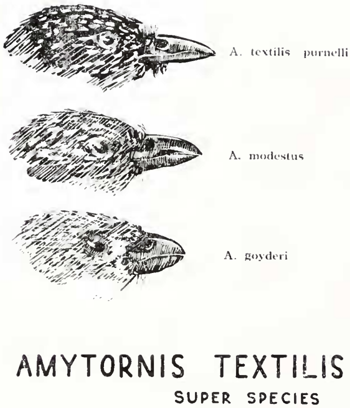

Fig. 17. Differentiation in bill form coincident with speciation in desert grass wrens of the *Amytornis textilis* group. The three species show successive stages in the transition from an insectivorous to a granivorous type of bill.

Amytornis provides one example of secondary overlap by newly evolved species: i.e., *A. modestus* and *A. textilis* in the Macdonnell Ranges. The two obviously originated in the east and west of the continent, respectively.

Geographic variation in the habitat occupied occurs in *Amytornis striatus* and *A. textilis* (Figs. 17a and 18a). The former, a widely distributed "parental" species occupying a range of habitats, has budded off a series of species around the periphery of its range that occupy rocky gorges only. In the *A. textilis* group there is the alternative situation of this species, occupying the western half of the continent, and the eastern *A. modestus*, each somewhat versatile in choice of habitat, separating out where their distributions meet. Thus, in the Macdonnell Ranges in central Australia, the former keeps to the rock surfaces of the gorges and plateaux and the latter to the areas of soft spinifex on the valley floor.

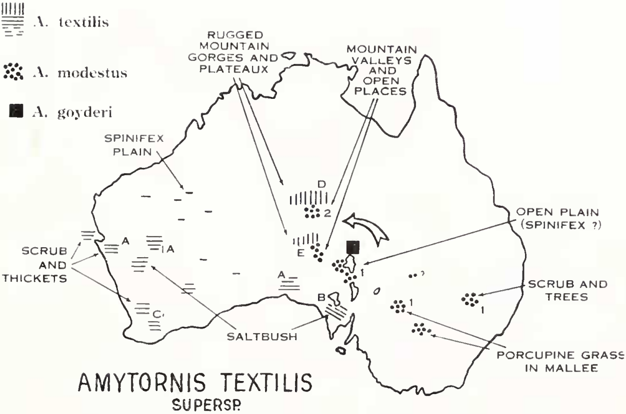

Fig. 17a. *Amytornis textilis* group of desert grass wrens. Distribution of species and their geographic variation in habitat is shown. The black square indicates the restricted range of the heavy-billed *A. goyderi* (now probably extinct.) *A. textilis* and *A. modestus*, relatively similar western and eastern counterparts, secondarily overlap in range (without interbreeding) in the mountains of central Australia. Each frequents a range of habitats except in the overlap zone, where one keeps to the rugged gorges and the other to the valleys. Here *A. modestus* is probably the secondary invader.

The letters refer to minor racial forms of *A. textilis*, and the numbers to those of *A. modestus*.

The isolated derivatives of *A. striatus* (*A. dorotheae*, *A. woodwardi*, and *A. housei*) could only have reached their present range at a time when desert (spinifex) replaced savannah grassland (an unsuitable habitat in that it lacks permanent cover).

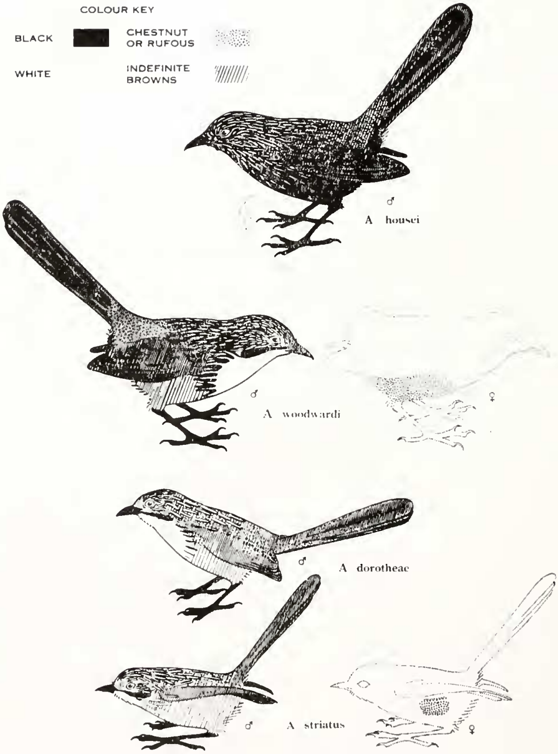

Fig. 18. Members of the *Amytornis striatus* superspecies to show the acquisition of striking size and colour differences. Though isolated, these forms have diverged morphologically to such an extent that there can be little doubt that they are genetic species.

Dasyornis: The two species, *D. broadbenti* and *D. brachypterus,* whose habitat is dense coastal undergrowth, have a discontinuous and relict distribution, each being isolated into two distinctive stocks, a southeastern and a southwestern one (see figure in Keast, 1957b). The southwestern forms are virtually extinct today.

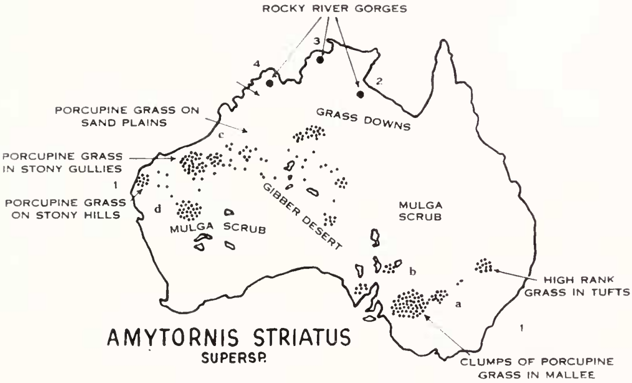

Fig. 18a. The range of the various forms in the *A. striatus* superspecies. The parental *A. striatus* (1, a-d) extends widely through the arid and semi-arid interior, whilst the distinctive derivatives *A. dorotheae*, *A. woodwardi*, and *A. housei* (2, 3, 4) are isolated in the rocky gorges of the McArthur, Alligator, and Charnley Rivers, respectively. The habitats occupied in different areas are shown on the outside of the map, vegetation formations that constitute distributional barriers on the inside.

The three northern species could only have reached their present position at a time when desert spinifex grassland was continuous through to the northern seaboard.

Stipiturus: A single superspecies is involved here, there being three major, isolated, stocks falling into two species. Their distribution is shown in Figure 19.

Stipiturus is an interesting genus in two ways: (a) because of the large number (5) of morphologically differentiated isolates in the species *S. malachurus.* These, occupying shrinking areas of specialized coastal habitat and cut off from the main stock in southeastern Australia, occur as follows:— Tasmania (*littleri*), Kangaroo Island (*halmaturinus*), Mount Compass area of South Australia (*intermedius*), southwestern Australia (*westernensis*), and Dirk Hartog Island (*hartogi*). (b) It provides an interesting demonstration of an ecological transition

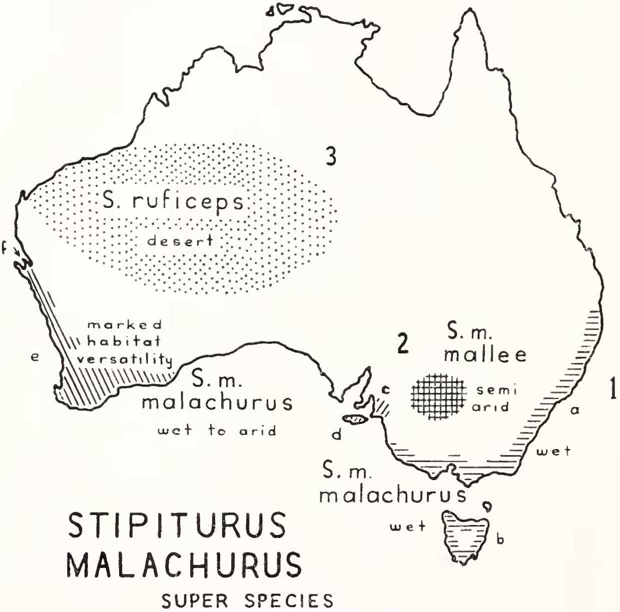

Fig. 19. Isolation, speciation, and habitat differentiation, in emu-wrens of the genus *Stipiturus*. *S. malachurus* (1), a secretive species requiring dense undergrowth, is broken up distributionally into a series of minor isolates around the periphery of the continent (see a-f).

Distributional barriers are areas of open country and sea. Distinctive isolated forms, approaching or that have reached species status (*S. malachurus mallee* — 2, and *S. ruficeps* — 3), occur in semi-arid and arid mallee and spinifex desert areas, respectively.

Eastern populations of *S. malachurus* are limited to sub-marshy areas, but in the southwest, where coastal undergrowth and spinifex lie in close proximity, adjacent populations demonstrate the complete ecological transition to life in arid places.

from life in well watered coastal areas to that in arid spinifex desert.

The three forms occupy quite distinct habitats: *S. malachurus*, submarshy coastal heathlands and thickets (basically), *S.(malachurus) mallee*, the mallee, and *S. ruficeps*, desert spinifex. *S. malachurus* does, however, vary geographically in the habitat occupied. In coastal New South Wales, Victoria, and Tasmania, submarshy areas of rank grass and heath (40-inch rainfall zone) are inhabited. On Kangaroo Island the habitat is dry undergrowth, including thickets on stony hills (25-inch rainfall zone). In the southwest of the continent the species extends from the coastal regions out through the regions of semi-arid to arid scrub and undergrowth towards the 10-inch rainfall isohyet.

Malurus: This genus with 12 Australian species forms a compact group. All are sedentary, somewhat gregarious, and occupy habitat of the shrub or rank grassland type in different parts of the continent. Speciation is actively occurring.

Malurus falls into five species groups: *M. cyaneus-melanotus-callainus-splendens*, *M. lamberti*, *M. leuconotus*, *M. melanotis*, and *M. coronatus*. The first two are particularly interesting from the viewpoint of speciation.

Malurus cyaneus-melanotus-callainus-splendens group of wren species (Fig. 8). These forms occupy broad, mutually exclusive zones and different habitats, from east to west across the continent. Three of the four have reached that stage of colour pattern differentiation typical of genetic species. The habitats occupied, however, the common denominator of which is dense shrubby cover, could be described as being as distinct in terms of vegetation type and climate as "proven" species in other genera. The only possible zone of contact between the four forms, however, is in New South Wales, where riverside thickets (occupied by *M. cyaneus*) and mallee (occupied by *M. melanotus*) approach each other. The relationship between habitat occupied and speciation in this and other groups is discussed in Section VII.

Within the *M. lamberti* group, distinct forms occupy the following areas of the continent (Fig. 20): (a) arid interior of continent (*mastersi*), (b) well-watered coastal fringe of New South Wales (*lamberti*), (c) mallee and creekside thickets in western New South Wales (*assimilis*), (d) high-rainfall coastal corner of southwestern Australia (*elegans*), (e) "intermediate" country in southwestern Australia and on Eyre Peninsula (*pulcherrimus*), (f) tropical Cape York (*amabilis*), (g) tropical northwestern Australia (*dulcior*). In addition there is a minor colour isolate on Bernier Island, northwestern Australia (*bernieri*).

Since the seven geographically representative forms largely replace each other, and have diverged only a minor to moderate extent morphologically, there has long been doubt as to their status. A field study in southwestern Australia by Serventy

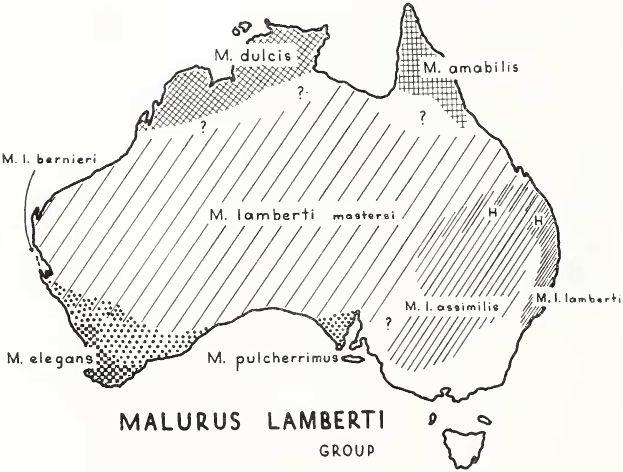

Fig. 20. Distribution of species and forms in the *Malurus lamberti* group of chestnut-shouldered wrens. Speciation and variation in this group are highly complex and incompletely understood.

In the southwest of the continent three distinctive colour forms, occupying adjacent zones behave as good species to each other. These are: *Malurus elegans, M. pulcherrimus,* and *M. lamberti mastersi.* Three colour forms in the east, also occupying zones of decreasing rainfall, intergrade where they meet (see H). These are the races *M. lamberti lamberti, M. l. assimilis,* and *M. l. mastersi.*

Two distinctive forms in the northwest and northeast of the continent are isolated from each other and, apparently, from the desert *mastersi.* Their genetic status is unknown but, in view of the fact that they differ to as great a degree as *elegans, pulcherrimus,* and *lamberti,* they are best regarded as taxonomic species.

The group thus contains three proven species, and possibly five.

(1951), however, has surprisingly demonstrated that the three forms occurring there (*elegans*, *pulcherrimus*, *lamberti mastersi*), despite being fairly similar in colour, overlap in range and behave as good species toward each other. In contrast with this situation, the three morphologically and ecologically equivalent forms in the east (*lamberti lamberti*, *l. assimilis*, *l. mastersi*) intergrade in southern Queensland where the dry country approaches the coast (Mack, 1934b). This contact is probably secondary.

The Cape York and Arnhem Land representatives of the group (*amabilis* and *dulcior*) live in relatively wet areas and are apparently isolated from the desert *mastersi* by a considerable range gap, deficient in ground cover. They are at least as distinct morphologically from each other and from *mastersi* as are *elegans* and *pulcherrimus*.

The evolutionary situation in the chestnut-shouldered wrens is thus a highly interesting one. There are three proven species, plus two isolated forms sufficiently distinct morphologically to suggest that they could not successfully interbreed.

The zonal nature of the distribution of *M. elegans*, *M. pulcherrimus*, and *M. lamberti mastersi*, in southwestern Australia is presumably a secondary phenomenon. *M. elegans* could, conceivably, have come from the east, colonizing around the coastline. *M. pulcherrimus* has an outlyer on Eyre Peninsula (i.e., like the other southwestern species *Climacteris rufa* and *Eopsaltria australis* [*griscogularis*].

The other species groups in *Malurus* have one morphologically differentiated isolate each, as follows: *M. leuconotus* (one on Dirk Hartog and Barrow Islands), *M. melanocephalus*, a species with an eastern and northern coastal distribution (one in northwestern Australia), and *M. coronatus* (one, possibly, in the country at the head of the Gulf of Carpentaria).

Speciation in the Subfamily Malurinae, Summarized

There are three instances of secondary range overlap by "newly evolved" species: *Acanthiza ewingi* — *A. pusilla diemenensis* in Tasmania, and *Malurus elegans* — *M. pulcherrimus* — *M. lamberti mastersi*, in southwestern Australia.

Isolates that have reached such a stage of morphological differentiation that they must be good genetic species occur as follows: *Gerygone*, 2; *Amytornis*, 4; *Stipiturus*, 1 or 2; *Malurus*, 4-5. Total: 11-13.

Morphologically differentiated isolates of lesser degree total 61 (Table 3), 16 of which could be said to have reached a moderate stage of differentiation. This is over one per species. It reflects the relatively poor dispersive capacities of the majority, their local habits, tendency to keep to dense cover, and fairly specific habitat requirements.

Hybrid zones occur in *Sericornis maculosa-frontalis*, and between the eastern forms in the *Malurus lamberti* complex.

Some 23 malurinid species do not vary geographically, but some 21 of these have such restricted ranges that this would not be expected, e.g., *Acanthiza ewingi*, *Origma rubecula*, and *Oreoscopus gutturalis*. The remaining two (*Epithianura tricolor* and *E. aurifrons*) are nomads.

Colour and size clines occur in several malurinid species, especially in those belonging to the genus *Acanthiza*. *Smicrornis brevirostris* has both. In the genus *Amytornis*, however, coincident with speciation, these trends may be reversed.

Gerygone magnirostris, *G. palpebrosa*, and *G. chloronota*, that extend through to New Guinea, have minor isolates in that region.

Family ARTAMIDAE
(Wood-Swallows)

The six Australian Wood-Swallows (4 of them endemic) are aerial feeders and hence are strong on the wing. Most of them range widely over the continent.

Speciation

The development of geographic variation in this group in association with seasonal movements has been reviewed by Keast (1958e). In only the single sedentary species (*A. cinereus*) is it marked, but isolation is lacking. Two migratory species have minor clinical variation, *A. leucorhynchus* and *cyanopterus*. The remainder, strongly nomadic species, do not vary at all geographically.

A. leucorhynchus, in an extra-Australian range extending from the Andamans and Philippines to Fiji and Palau, has some 9 distinctive isolates.

Family SITTIDAE
(Nuthatches and Australian Tree-Creepers)

This family, as now constituted (Mayr and Amadon, 1951), contains two genera in Australia, *Climateris* and *Neositta,* ecological counterparts, respectively, of the creepers and nuthatches of the Palaearctic. The species are highly specialized ecologically, gaining their insect food from fissures and cracks in the trunks and branches, though some members of *Climacteris picumnus* group have taken secondarily to feeding from the ground. *Climacteris* has six species in Australia, one extending to New Guinea. *Neositta* is now regarded as being composed of only one species (Mayr, 1950b — See Figure 21).

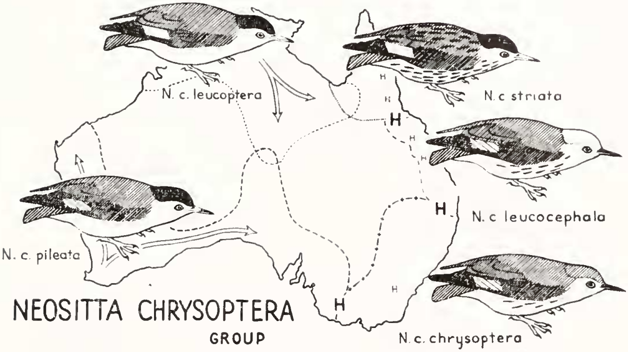

Fig. 21. *Neositta chrysoptera* superspecies, a case of multiple hybridization at contact fronts (Mayr, 1951). In this case distinctive forms have developed in various parts of the continent, including the southwest, northwest, Cape York, central Queensland, and southeast. Secondarily, however, outward extension of range has occurred, particularly from the northwest and southwest (see white arrows). Zones of hybridization (see letters H) connect a number of the forms today.

Neositta is significant in two ways: as an example of multiple hybridization, and in that relatively great morphological differences have been attained without reproductive isolation. Thus, head colouring may be brown (indicated by close cross-hatching), black, or white. Body striations may be absent. The bill may be black or yellow. The wing bar may be orange (sparse cross-hatching) or white.

Climacteris has species in a range of habitats but *Neositta* is essentially a species of sclerophyll forests and savannah. All species are sedentary.

Speciation

Climacteris is composed of three species groups (Keast, 1957e). Most interesting of these is the *C. picumnus* group of savannah woodland species and forms (Fig. 22). *C. picumnus* proper inhabits the southeast and its distinctive isolate, *C. picumnus melanotis*, the northeast. *C. rufa*, an isolate so distinctive that it must be regarded as having reached species status, occupies the southwest and has a minor derivative on Eyre Peninsula. *C. melanura* inhabits the northwestern sector and has a derivative (*wellsi*) in the Hamersley section of the central west. There

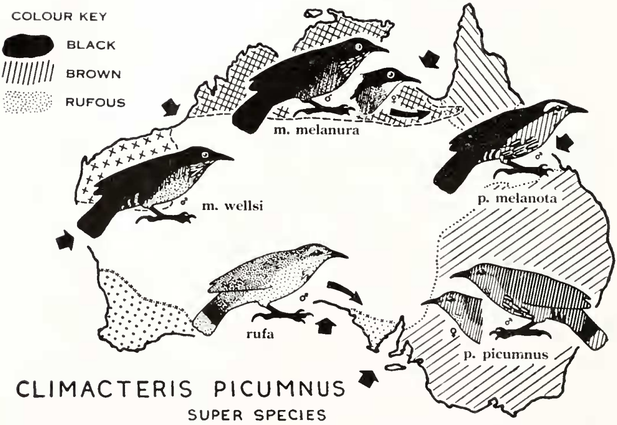

Fig. 22. Isolation and speciation in the *Climacteris picumnus* group of savannah-dwelling tree-creepers. There is a distinctive form corresponding to each of the major savannah woodland belts on the continent. In contrast with *Neositta*, though there has been outward range spread, secondary contact has occurred only in the north. Here, however, there is no hybridization, showing that specific distinctness has been attained.

The southwestern form, *C. rufa*, can, in view of its distinctiveness, best (from the taxonomic point of view) be regarded as a species.

The black arrows on the outside of the map indicate the distributional barriers, each a dry to arid section from which the necessary habitat is absent. The arrows within the map indicate major secondary range extensions.

is thus a chain of six forms, each centred on a hilly or mountainous "refuge" area. All remain isolated except at the head of the Gulf of Carpentaria where *C. melanura* has secondarily extended its range to meet and co-exist with *C. picumnus melanotis*, without interbreeding. Within the group there is, accordingly, the full range of stages in the speciation process from minor isolates to a newly-evolved species.

C. leucophaea, making up the second species group is a montane species in New Guinea (3 isolates), and a rain forest-sclerophyll forest species in eastern Australia. Here it has two morphologically differentiated isolates, a distinctive one in the Cairns-Atherton region (*minor*), and a lesser one in the Mount Lofty Ranges (*grisescens*). The third species group is composed of two species, *C. erythrops* (inhabiting mountain sclerophyll in the east) and *C. affinis* (mulga desert).

Climacteris provides one of the best demonstrations of differentiation and speciation in refuge areas. These same tracts of country also function as refuge areas in other groups, e.g. parrots, nuthatches.

Neositta provides a most interesting contrast with *Climacteris* in that (though differentiation has again occurred in these refuge areas) the various isolates have secondarily reunited to form hybrid zones (Mayr, 1950b). The genus has a chain of forms around the periphery of the continent, as follows: southeast (*chrysoptera chrysoptera*), southwest and south (*pileata*), northwest and north (*leucoptera*), northeast (*striata*), central east (*albata, leucocephala*, etc). *Neositta* provides a splendid example of multiple hybridization (intergradation) along contact fronts (see Section X), and is surprising for the degree of differentiation achieved without the attainment of reproductive isolation. The morphological characteristics, ranges, and approximate areas of hybrid zones in *Neositta* are shown in Figure 21. Differentiation of forms has occurred in the same areas as in *Climacteris*, except that *Neositta* lacks them in the Hamersley and Eyre Peninsula sectors and has several in eastern Queensland.

Clinal variation occurs in various Australian Sittidae.

Family DICAEIDAE
(Flower-seekers and Pardalotes)

This family, in Australia, falls into two genera, the endemic and somewhat aberrant *Pardalotus* (7 species) and *Dicaeum* (1 species). The latter is well developed in southeastern Asia, Indonesia, New Guinea, and islands of the western Pacific. *Dicaeum hirundinaceum*, the Australian representative, is itself the end member of a superspecies extending through from Asia.

Pardalotus occurs throughout Australia. *P. punctatus* inhabits the sclerophyll forests of eastern and southern Australia and has given rise to *P. quadragintus* in Tasmania and to the mallee species, *P. xanthopygus*. *P. melanocephalus* mainly inhabits the tropical savannah woodlands. *P. rubricatus* is a savannah grassland-arid country species. The remaining species live in dry sclerophyll forest and savannah woodland, with a distinct tendency to occur along rivers. *Dicaeum hirundinaceum* occurs throughout the continent and has an extremely wide habitat tolerance.

Dicaeum is highly nomadic. *Pardalotus striatus* has a south-north migration. Other pardalotes, inhabiting the dryer areas, are apparently partial nomads.

Speciation

Pardalotus contains an instance of speciation by double invasion (into Tasmania), *P. quadragintus* representing the earlier, and the endemic race of *P. punctatus* (*leachi*) the later one. Apart from this, the only differentiating isolates in the group are the insignificant southwestern form of *P. punctatus* and the northwestern one of *P. melanocephalus*.

The puzzling status and relationships of *Pardalotus substriatus*, *P. ornatus*, and *P. striatus*, largely geographically representative forms recognizable only on minor grounds, have been discussed by Hindwood and Mayr (1946) and Serventy (1953). The first of these extends widely across the southern two-thirds of the continent, the second through a broad south-north zone in the east, and the third is confined to Tasmania and the southeastern coastal strip of the mainland. The three overlap in eastern Australia but, despite their morphological similarity and the absence of habitat differences between them, only 1.8 per cent of the specimens are morphologically intermediate, i.e. hybrids, according to the findings of Hindwood and Mayr. Serventy (1953), however, interprets the evidence differently, saying that *ornatus* is itself nothing but a hybrid form. He also draws attention to the existence of a specimen from southwestern Australia that has a yellow wing speculum (a characteristic of the southeastern *striatus*) as indicating the presence of occasional genes of that species in the far west. Serventy suggests that all the "striped-crowned" pardolates, hence, probably belong to a single species. In any event, there can be little doubt that *P. substriatus* originated in southwestern Australia and *P. striatus* in Tasmania. A high proportion of the latter occurring in eastern Australia are winter migrants.

P. melanocephalus is the northern representative of the group. It obviously originated in the northwest or north and has secondarily spread southwards to overlap the range of *P. substriatus.*

The ecology of *Dicaeum hirundinaceum*, its intimate relationship with the mistletoes (Loranthaceae), and the influence of these on its potential for developing geographic variation have been discussed by Keast (1958d). *Loranthus* berries form the main food of *Dicaeum*, and the bird undertakes extensive seasonal movements coincident with the fruiting of the plants. This may be in spring, summer, autumn, or winter, in different areas. Its breeding is also linked to the berry crop. The occurrence of mistletoes in all the main forest and scrub associations explains the wide range of vegetation formations inhabited by *Dicaeum.* The bird is a major disseminator of *Loranthus.*

D. hirundinaceum has only negligible geographic variation in Australia. Where, however, the nomadic habit has been lost (i.e., in the colonizing of the Aru, Kei, and Tenimber Islands), distinctive insular isolates occur.

Family MELIPHAGIDAE
(Honeyeaters)

This is an Australo-Papuan family of about 150 species, some 67 of which occur in Australia. Their common character is the brush-tongue and, though primarily insectivorous, nectar is prominent in the diet.

Of the 20 or more genera occurring in Australia, 12 obviously originated here: *Melithreptus, Plectorhynchus, Certhionyx, Acanthorhynchus, Gliciphila, Ramsayornis, Granticlla, Conopophila, Zanthomiza, Phylidonyris* (with *Meliornis*), *Manorina* (with *Myzantha*), and *Anthochaera-Acanthagenys.*

At the species level all are apparently Australian with the exception of about 18 that are recent immigrants from New

Guinea, or are obviously derived from such. The majority of the 23 species of the large genus *Meliphaga* occurring in Australia are endemic.

Honeyeater species are specialized for life in the full range of vegetation formations and the degree of ''habitat tolerance'' of any one is commonly limited. Many species are sedentary but ''blossom nomadism,'' of limited amplitude, is widespread. A few species, especially *Grantiella picta*, *Certhionyx variegatus*, *Myzomelia nigra*, are highly nomadic. *Meliphaga chrysops* and *Melithreptus lunatus* are partial south-north migrants in the southeastern part of their range.

Speciation

The Australian Meliphagidae contain examples of a wide range of speciation phenomena, including two instances of triple invasion, one of re-invasion, and several demonstrations of secondary range overlap by recently evolved species. There are a considerable number of minor instances of isolation and differentiation.

(a) Instances of Recently Completed Speciation and some Special Phenomena

(i) *Melithreptus lunatus* and *M. albogularis*, a case of secondary range overlap in peripheral sclerophyll-savannah woodland species (Fig. 23). These two species are so similar that, if they did not co-exist over an extensive area, they would rank as no more than minor geographic races. Both are strictly peripheral in range, inhabiting sclerophyll forest and savannah woodland. *M. lunatus* is southern and eastern in distribution, *M. albogularis* northern and eastern. The overlap area extends from Cairns to the Richmond River, a distance of 1,000 miles (Fig. 23).

Interest in this case lies in: (a) circumstances of the original isolation and hence speciation; (b) how it is possible for two such similar species to co-exist.

There can be little doubt that *M. albogularis* developed in the Kimberley-Arnhem Land sector of the northwest, that is to the west of the Gulf of Carpentaria. A recent eastward extension of range by various northwestern bird species and races has been noted (Keast, 1956a). *M. albogularis,* however, has followed this with a great range extension southwards through the coastal forests of eastern Queensland.

Fig. 23. Speciation in the *Melithreptus lunatus* group of savannah woodland — sclerophyll forest honeyeaters.

M. lunatus (1 — stippled areas) is related to the others as follows: *M. albogularis* (2—see cross-hatching), barely distinguishable on morphological grounds, mainly inhabits the north of the continent but overlaps the range of *M. lunatus* in eastern Australia by about 1,000 miles. *M. affinis* (3 — range shown in black), is a distinctive Tasmanian isolate. *M. lunatus chloropsis* (4 — heavily spotted area), a long-billed isolate in the southwest, has reached a lesser degree of divergence.

There can be no doubt that the sibling species *M. albogularis* originated in northwestern Australia (or possibly even New Guinea) and that its occurrence in eastern Australia is secondary. In at least part of the overlap area it occupies a different habitat to *M. lunatus*.

M. lunatus and *M. albogularis* occupy slightly different areas in the overlap zone. The former occurs only on the tops of the ranges and the latter only in the lowlands (Barnard and Barnard, 1925; Barnard, 1926). Several other southern bird species are restricted to the higher country in the northern parts of their range, e.g., *Meliphaga lewini* and *Dacelo novaeguineae*. In colonizing southwards, *M. albogularis* may accordingly have been able to move, partly unimpeded by competition, through the lowlands.

The fleshy orbital ring is a vivid orange colour in the eastern race of *M. lunatus*. In other members of the genus, and in the southwestern race of this species, this area of the body is a drab white, greenish, or pale blue colour. The character could have an important role in helping to prevent hybridization with the superficially similar *M. albogularis*.[1]

(ii) *Meliphaga lewini*, *M. notata*, and *M. gracilis*, a case of triple invasion by rain forest species from New Guinea (Fig. 24). These three species have the same colouration and colour pattern and obviously are derived from a common New Guinea stock. The chief differences are in size, *M. lewini* being the largest and *M. gracilis* the smallest, and in the relatively long bill of *M. gracilis*. *M. lewini* does not have a close counterpart in New Guinea, whereas *M. notata* shares a semi-species relationship with *M. analoga* there (Rand, 1936), and *M. gracilis*, in Australia, is only racially distinct from its parental form.

M. lewini, the species with the southernmost range (Dandenongs to the Cairns-Atherton area), has obviously had a fairly long history in Australia. By contrast, the bifurcation of *analoga-notata* from *gracilis* must have taken place in New Guinea. *M. notata* and *M. gracilis* are now each broken up into two populations in Australia, inhabiting the Cape York and Cairns rain forests, respectively.

Where the three species overlap, *M. lewini* occupies the highlands and *M. notata* the lowlands (Barnard, 1926). The long-billed *M. gracilis* is also a lowland dweller.

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[1] Brown and Wilson (1956) might regard this as an example of a character being modified as the result of contact between two closely related species. Against this, however, is the argument that the red orbital ring is typical of *M. lunatus* throughout its eastern range, not just where it meets *M. albogularis*. There would seem to be no doubt that the latter is the invader.

Actually there is relatively little evidence of modification to, or reinforcement of, a morphological character in zones of contact between closely related species in Australian birds — though see *Meliphaga virescens-versicolor*.

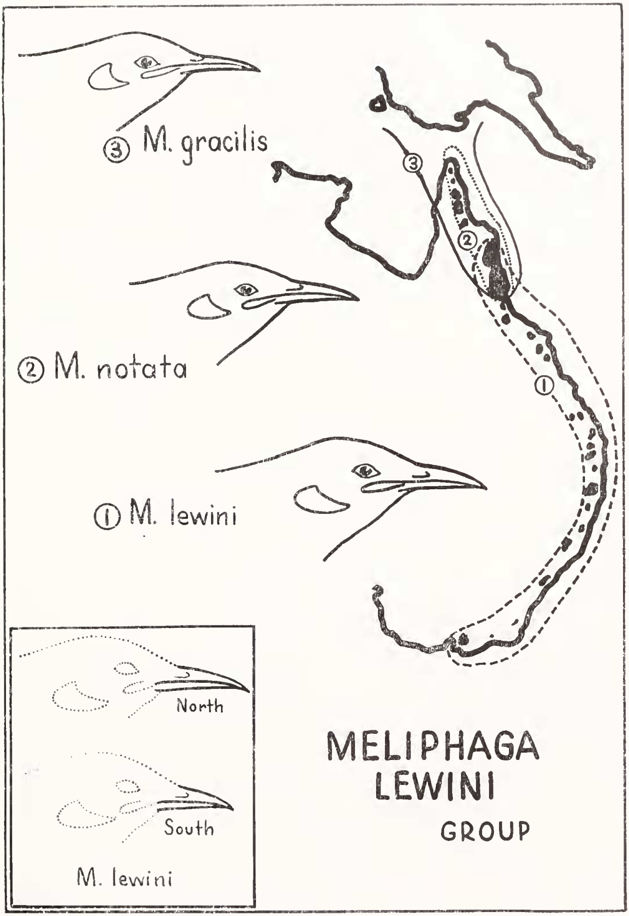

Fig. 24. Triple invasion of Australia by similarly coloured New Guinea rain forest honeyeaters of the *Meliphaga lewini — notata — gracilis* group. The distinctive endemic species *M. lewini* (1) obviously represents the first wave. *M. notata* (2), the second arrival, ranks as a semi-species with *M. analoga* of New Guinea. *M. gracilis* (3), the most recent arrival, is only racially distinct from its New Guinea parent.

M. lewini and *M. notata* occupy different sub-zones where they overlap, the former keeping to the highlands and the latter to the lowlands. *M. lewini* has a south-north cline of increasing bill length and decreasing wing length.

(iii) *Meliphaga virescens* and *M. versicolor*, a case of speciation in New Guinea and reinvasion of the Australian continent into a new habitat (Fig. 25).

Fig. 25. *Meliphaga virescens* superspecies, a case of speciation by "reinvasion." The parental species has a wide range through the arid interior of Australia. It only enters mangroves in the west where conditions are dry. The New Guinea derivative, *M. versicolor,* has re-invaded the continent (see black arrows) to colonize the unoccupied eastern mangroves. It does not go beyond the forest fringes adjacent to the mangroves and hence has a range parallel to, but not overlapping, that of *M. virescens.*

The dotted arrows indicate the range of an earlier specialized derivative, *M. fasciogularis,* a species inhabiting the more southern mangroves of eastern Australia.

The numbers indicate geographic races of *M. versicolor.*

M. virescens, a widely ranging savannah grassland-mulga species, varies clinally in colour and size. *M. versicolor* has three forms, one inhabiting northern New Guinea that is barely distinguishable from typical *virescens*, one in the Milne Bay area that is intermediate, and one in southern New Guinea and Cape York that has accentuated colouring and is markedly distinct from *virescens*. Nevertheless, all would rank as one species were it not for the fact that *M. virescens* and *M. versicolor* occur together, without interbreeding, on Cape York.

M.versicolor obviously represents a branch of *M. virescens* that became isolated in New Guinea and there built up genetic and morphological differences from the parental stock. The habitat relationships of the two are interesting. *M. virescens* extends throughout the dry parts of the continent but does not penetrate into the wet eastern coastal strip. In the dryer west, however, it does occupy mangroves. On Cape York it is confined to the dryer savannahs of the western side. *M. veriscolor*, a coastal species in New Guinea, has invaded Australia into the offshore mangroves of eastern Cape York.

The mangroves of southeastern Queensland are occupied by a third related species, *M. fasciogularis*. This is isolated from *M. virescens* by the wet coastal forests but overlaps *M. versicolor* in range without interbreeding.

(iv) *Philemon argenticeps* and *P. novaeguineae*, a case of triple invasion from New Guinea (Fig. 26).

The friarbird *Philemon* (*moluccensis*) *novaeguineae* has a wide distribution through the islands to the north of Australia. It has invaded the Australian continent three times, the earliest wave giving rise to the savannah dwelling *P. argenticeps*, and subsequent ones to *P. novaeguineae gordoni* and *P. n. yorki* in the mangroves (mainly) of Arnhem Land and coastal savannah woodlands of Cape York, respectively. The degree of morphological distinctness of the forms is only moderate and were it not for their co-existing they would only rank as races (Mayr, 1944a, p. 167). *P. argenticeps*, the earliest arrival, is now well adapted to the dry country and extends well south into it.

(v) Dry country *Meliphaga* species of the *cratitia-plumula-ornata-keartlandi-flavescens-fusca* groups, examples of "refuge area" differentiation and speciation.

These species fall into two or three species groups, the members of each of which tend to occupy different segments of the fairly

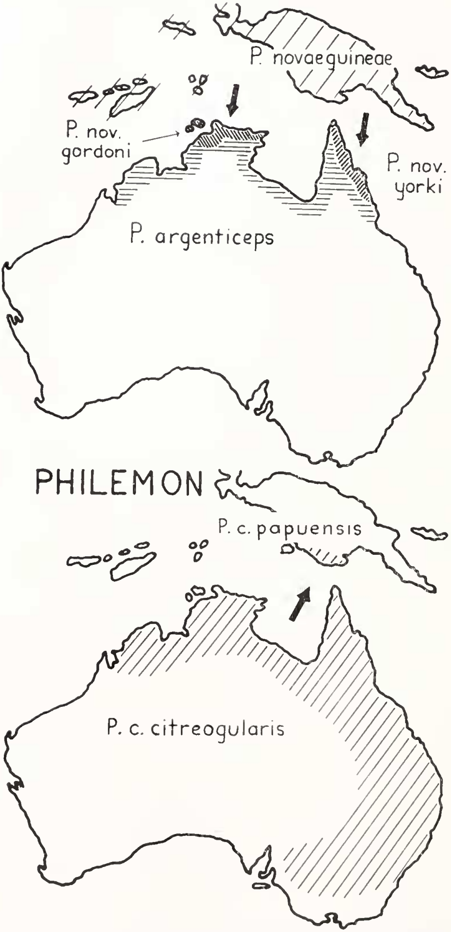

Fig. 26. Speciation in the genus *Philemon* (Meliphagidae). *P. novaeguineae* has invaded Australia from the north three times. The first colonization (now *P. argenticeps*), adapted to dry savannah forest, has reached specific distinctness, as shown by its non-hybridization with later arrivals. Subsequently, there have been parallel waves of colonization into the northwest and northeast, respectively (*novaeguineae gordoni* and *n. yorki*). The latter two keep to the mangroves and wetter coastal savanah.

The lower map demonstrates a case of the reverse process, colonization of the savannah woodland areas of southern New Guinea by the Australian savannah species, *Philemon citreogularis*. The insular population has now reached race status.

dry (mainly savannah woodland-grassland) parts of the continent. Their ranges, however, may be marked by broad overlaps today. Habitat differences are often present but ill-defined, with equivalent plant associations being occupied by different species as between north and south, or east and west.

Current distribution patterns indicate that species arose in the east (*fusca*), north (*flavescens*), and south (*cratitia*, *ornata*) of the continent.

(vi) *Myzantha flavigula* and *M. melanotis* in the Victorian mallee.

This puzzling case has been discussed by Serventy (1953). In southwestern Australia the widely ranging, savannah woodland-grassland *M. flavigula* is connected clinally with a darkly pigmented race in southwestern Australia (*obscura*), inhabiting the coastal high rainfall zone. In the Victorian mallee, however, where a similar colour form (*melanotis*) occurs, it behaves as a distinct breeding unit co-existing, but not hybridizing, with *M. flavigula*.

The circumstances of the original isolation of *M. melanotis* are obscure, unless the species is of southwestern origin.

(vii) The semi-species *Meliphaga melanops* and *M. cassidix*, secondary contact without interbreeding.

These two species are so similar morphologically that they can only doubtfully be distinguished in the field. *M. melanops* has a fairly wide range in the sclerophyll forests of eastern Australia and it approaches and apparently meets *M. cassidix* (restricted to the Dandenong region of Victoria), along the periphery of its range without interbreeding — see analysis of Wakefield (1958). *M. melanops* is apparently a secondary invader of southern Victoria.

(b) Morphologically Differentiated Isolates

The following are examples of geographically representative species, i.e., isolates that are so distinctive that they must now be genetic species:

(i) *Anthochaera paradoxa* (Tasmania). Parental stock: *A. carunculata* inhabiting the sclerophyll forests of southern Australia.

(ii) *Meliphaga flavicollis* (Tasmania). Parental stock: *M. leucotis*, inhabiting sclerophyll and mallee in southern Australia.

(iii) *Melithreptus affinis* (Tasmania). Parental stock: *M. lunatus* of the sclerophyll forests of southern Australia.

(iv) *Melithreptus validirostris* (Tasmania). Parental stock: *M. gularis*, inhabiting savannah woodland and dry sclerophyll in southern Australia. This form is somewhat less distinctive than the others and is probably not specifically distinct.

(v) *Acanthorhynchus superciliosus* (sclerophyll forests of southwest corner). Parental stock: *A. tenuirostris* of southeastern and eastern sclerophyll forests.

(vi) *Meliphaga notata* (rain forests of northeastern Australia). Parental stock: *M. analoga* of New Guinea (see previous discussion).

(vii) *Meliphaga macleayana* (Cairns-Atherton rain forests). Parental stock: *M. chrysotis* of New Guinea, now secondarily established in the rain forests of Cape York.

The total number of morphologically differentiated isolates in the Australian Meliphagidae will be seen in Table 3. These, if geographically representative species are excluded, total 18, and occur in 12 species, as follows:

Melithreptus lunatus, sclerophyll forest, 1, well differentiated; *Myzomela erythrocephala*, rain forest and mangroves, 1, major form; *M. obscura*, rain forest and mangroves, 1, minor form; *Acanthorhynchus tenuirostris*, sclerophyll forest, 2, minor forms; *Meliphaga notata*, rain forest, 1, minor; *M. gracilis*, rain forest, 1, minor; *M. flavescens*, tropical savannah woodland, 2, both minor; *Phylidonyris pyrrhoptera*, sclerophyll, 2, both minor; *P. novae-hollandiae*, sclerophyll, 1, minor; *P. niger*, sclerophyll, 1, minor; *Anthochaera chrysoptera*, sclerophyll, 2, one major, one minor; *A. carunculata*, sclerophyll, 1, minor; *Entomyzon cyanotis*, savannah woodland, 1, minor; *Philemon novae-guineae*, savannah woodland and mangroves, 1, minor.

Some 23 honeyeater species do not vary geographically in size or colour. Some 14 of these, however, are either insular species or have ranges so restricted that this would not be expected. About 5 are highly nomadic and several are partial nomads. *Melithreptus albogularis* has radiated outwards only fairly recently.

Speciation across Torres Strait has figured fairly prominently in the building up of the Australian honeyeater fauna though, proportionately, to a much less degree than in the Muscicapinae. *Philemon citreogularis* (Fig. 26), *P. corniculatus*, and *Meliphaga flavescens*, by contrast, are Australian savannah woodland species that have given rise to forms in southern New Guinea.

Hybrid zones do not occur in the Meliphagidae, though the relationships of the northern and southern forms in *Melithreptus gularis* merit investigation.

As noted, relatively few of the Australian Meliphagidae extend beyond the continent, but those that do tend to have morphologically differentiated insular isolates. Thus, *Myzomela dibapha* has about eight, mostly in the Celebes-Timor sector but with one on New Caledonia. *Lichmera indistincta* falls into many forms (over 5) in a range extending from Timor to the southwest Pacific. Other species have minor isolates in New Guinea.

Clines are common in the Meliphagidae, with most being demonstrations either of the Bergmann or Gloger effects. *Meliphaga lewini*, however, has a south-north cline of increasing bill length. The "plastic" interior species, *M. virescens,* provides examples of somewhat complicated colour variation. In *Melithreptus gularis* and *Meliphaga penicillata*, as in *Smicrornis brevirostris*, three colour forms extend in broad zones from east to west across the continent. As noted, they are associated with specific rainfall and temperature threshholds.

Family ZOSTEROPIDAE
(White-eyes)

Of three Australian species of *Zosterops*, *Zosterops lateralis* is equally well developed on the continent and in the southwest Pacific, and the other two (*Z. lutea* and *Z. chloris albiventris*) are derived from island species to the northwest of the continent.

Z. lateralis has an eastern and southern distribution in Australia and is essentially an inhabitant of sclerophyll forest and rain forest. *Z. lutea*, inhabiting the north and west, is a mangrove dweller. *Z. chloris albiventris* is confined to the islands off Cape York.

The species are sedentary except that *Z. lateralis* has a limited south-north migration in the southeast of the continent.

Speciation

Z. lateralis has morphologically differentiated isolates in southwestern Australia (*gouldi*) and on the Capricorn Islands off eastern Queensland and Lord Howe Island (*tephropleura*). The Tasmanian form (*tasmanica*), also occurring in southern Victoria, and that occupying the Murray Valley (*halmaturina*), apparently former isolates, are now connected with nominate *lateralis* (eastern New South Wales) by minor zones of intergradation. The Cairns-Atherton form (*vegeta*) may also be an isolate. *Zosterops lutea* has forms in the Hamersley and Kimberley segments that are probably isolates. There is clinal variation in both.

Z. lateralis tasmanica has invaded New Zealand and thence Norfolk Island, the Chathams, and Campbell Island, within recorded history. The species has some 6 morphologically differentiated isolates in the southwest Pacific.

The successive invasions of Lord Howe Island and Norfolk Island by members of the genus *Zosterops* provide some of the classic cases of speciation by multiple invasion. Whether or not these forms, however, came from a single point source is doubtful.

Family PLOCEIDAE
Subfamily ESTRILDINAE
(Finches)

Of the 18 species composing the Australian Estrildinae only two, and possibly three, are derived from outside of the continent. *Lonchura flaviprymna,* inhabiting a restricted area in the northwest, is an isolated derivative of *L. maja* of Indonesia, and *Erythrura trichroa* has recently colonized Cape York from New Guinea. *Lonchura castaneothorax* has a wide range in New Guinea (two morphologically differentiated isolates) as well as in Australia.

The seed-eating finches are mainly inhabitants of the dryer creekside thickets and savannahs of the north and east. *Zonaeginthus bellus-oculatus,* by contrast, is confined to thickets in the sclerophylls of the south, *Estrilda temporalis* to the sclerophyll and rain forests of the east, *Lonchura castaneothorax* to reedbeds and areas of rank grass (east and north), *Zonaeginthus pictus* to rocky outcrops in the central desert, and *Erythrura trichroa* to rain forest fringes in the northeast. Whilst none of the finches undertake regular seasonal movements, those inhabiting the central and northern regions are somewhat sensitive to shifts in the supply of seeds and surface water, bad seasons forcing groups to move to new areas.

Speciation

Zonaeginthus bellus is represented by a form in southwestern Australia so distinct that it can best be regarded as having reached species status (*oculatus*), whilst in the northwest and northeast of the continent, *Poephila acuticauda* and *P. cincta* are counterparts of each other (see figs. in Keast, 1958f).

Isolates that have reached a moderate or lesser degree of differentiation occur in *Poephila personata* and *Lonchura castaneothorax* (as between Arnhem Land and Cape York), in *Estrilda temporalis* (in Cape York and Mount Lofty Ranges), and in *Poephila phaeton*. In the last named, the black-breasted nominate form, occupying coastal northern Australia, but not Cape York, has given rise to a white-breasted isolate in New Guinea (*evangelinae*) which, in turn, has invaded Cape York to give rise to a derivative there (*albiventer*). This latter remains isolated.

Isolation without differentiation can be seen in the Tasmanian population of *Zonaeginthus bellus* and in the Australian population of *Erythrura trichroa.*

Hybrid zones occur in *Poephila bichenovii* and in *Poephila cincta.* In the former, the hybrid zone, between northwestern and eastern stocks, is in the general region of Alexandria to the west of the Gulf of Carpentaria (Fig. 2 in Keast, 1958f). In the latter, it occurs at the base of Cape York between a form that developed on the peninsula and an eastern Queensland one (Fig. 3, same paper).

Clinical variation occurs in many finch species. Of those that do not vary geographically (8) most have relatively restricted ranges. *Poephila guttata*, with an almost Australia-wide distribution, is an exception. It has, however, distinctive insular isolates on Timor and Sumba. *Erythrura trichroa* has 8 insular isolates beyond Australia.

The number of morphologically differentiated isolates in the Australian finches is 6 within the continent and 12 outside of it.

Family ORIOLIDAE
(Orioles)

Two genera occur in Australia: *Oriolus* (2 species) and the endemic Australo-Papuan *Sphecotheres* (2 species). The group is restricted to the savannahs (mainly) and sclerophyll and rain forests of the east and north. A certain amount of nomadism occurs in *Oriolus sagittatus*.

Speciation

O. sagittatus and possibly *O. flavocinctus* are divided into two recognisable stocks occupying the east and northwest of the continent, respectively. Both species, and *Sphecotheres vieilloti*, have isolates in southern New Guinea.

Family DICRURIDAE
(Drongos)

Only one member of this Palaearctic family reaches Australia. *Dicrurus bracteatus* does not vary geographically. It has about three morphologically differentiated isolates in New Guinea.

Family CRACTICIDAE
(Australian Butcherbirds and Magpies)

This small Australo-Papuan family is composed of 3 genera and 10 species. All are Australian except 2, which are confined to New Guinea. Three species are shared by New Guinea and Australia.

The cracticids, predators with body sizes ranging from that of a shrike up to that of a crow, include some of the most prominent elements of the Australian countryside, the magpies, currawongs, and butcherbirds. A generalized habitat, extending from sclerophyll forest to semi-arid country, is typical of *Gymnorhina* and most species of *Cracticus*. *Cracticus quoyi* and *Strepera graculina* are, however, restricted to mangroves and sclerophyll forest, respectively. *S. versicolor* has a southern peripheral distribution with sclerophyll forest, savannah woodland, and mallee being occupied.

None of the Cracticidae undertake seasonal movements other than those of a local nomadic nature.

Speciation

The amount of geographic variation in the Australian Cracticidae is great, especially in view of the relatively large body size. There are some 10-12 isolates of varying degrees of differentiation within the confines of the continent.

Tasmania has two isolates so distinct that they must be regarded as approaching, if they have not already reached, the status of genetic species: *Strepera* (*graculina*) *fuliginosa* and *S.* (*versicolor*) *arguta*. The southwestern isolate of the magpie, *Gymnorhina* (*hypoleuca*) *dorsalis*, is also generally recognised as having achieved that degree of morphological differentiation typical of a species. Lesser isolates occur in *Cracticus torquatus* (Tasmania), *C. quoyi* (eastern Cape York), *Gymnorhina tibicen* (2, one of Groote Eylandt and the other in the Macdonnell Range section of the continent), and in *G. hypoleuca* (Tasmania) (Amadon, 1951).

By far the most interesting species, from the viewpoint of differentiation in isolation, is *Strepera versicolor*. It has isolates in the Everard-Musgrave Ranges of central Australia (*centralia*), southwestern Australia (*plumbea*), and on Eyre Peninsula (*intermedia*), the last separated from the nearest relative (to the east) by a mere 20-mile wide water gap. Forms in southeastern South Australia (*melanoptera*) and in the Victorian mallee (*howei*) are now, apparently, secondarily connected with each other, and with the nominate form to the east, by minor hybrid zones.

Beyond the confines of the continent, *Gymnorhina tibicen* has a morphologically differentiated isolate in southern New Guinea, and *Strepera graculina* has one on Lord Howe Island.

Gracticus mentalis, possibly the most primitive member of its genus (Amadon, 1951), has presumably invaded Cape York from New Guinea where it now co-exists with *C. torquatus*. If this species is, in fact, its nearest relative this is the only demonstration of the final stage in the speciation process to be found in the Cracticidae.

Hybrid zones occur between the "species" *Gymnorhina hypoleuca* and *G. tibicen* in southern New South Wales-northern Victoria, and between the races of *Strepera versicolor* in eastern South Australia-western Victoria. It is probable, moreover, that the intergradation between forms within *Cracticus torquatus* and within *C. nigrogularis*, in the north and west of the continent, is also secondary. The hybrid zone between *Gymnorhina hypoleuca* and *G. tibicen*, extending as it does almost throughout the length of the Murray Valley (some 800 miles) requires proper study to determine whether or not it is stable or whether one form is extending at the expense of the other.

Colour and size clines occur in mostly widely ranging members of the Cracticidae within Australia (see Amadon, 1951).

Family GRALLINIDAE
(Mud-nest Builders)

The species composing the Australian mud-nest builders fall into three monotypic genera: *Grallina cyanoleuca*, *Struthidea cinerea*, and *Corcorax melanorhamphos.* A fourth member of the group, *Pomareopsis bruijni,* is confined to New Guinea.

Speciation

None of the Australian Grallinidae vary geographically.

Family PTILONORHYNCHIDAE
(Bower-birds)

The bower-birds are purely an Australo-Papuan group, with 6 species being confined to Australia, 9 to New Guinea, and 2 being shared.

The Australian species occupy a range of habitats from the dry interior to the eastern rain forests. The latter vegetation association is richest in species. Two species, the monotypic *Scenopoeetes dentirostris* and *Prionodura newtoniana,* are restricted to the highlands of the Atherton rain forest tract. There are no bower-birds in Tasmania.

Seasonal movements in the bower-birds are restricted to a local nomadism that has little effect on speciation trends.

Speciation

There are no instances of recently completed speciation in terms of range overlap by closely related species. All degrees of differentiation in isolation, however, occur (Mayr and Jennings, 1952). The rain forest species *Ptilonorhynchus violaceus* and *Ailuroedus crassirostris,* restricted to eastern Australia, each have distinctive southern and northern forms that are isolated from each other. The southern form of the latter is approaching that stage of differentiation typical of a species. In both cases the range gap is about 600 miles. Within the savannah grassland *Chlamydera maculata* there are eastern (*maculata*) and western (*guttata*) forms isolated by the general Simpson desert area along the eastern border of South Australia. These two are approaching, or have reached, that stage of differentiation typical of species. Here the range gap is apparently 400-500 miles. In *C. nuchalis* western and eastern forms are connected by a marked step in a cline (western

Queensland), indicating secondary intergradation between previously separated populations (Mayr and Jennings, 1952).

The savannah woodland *Chlamydera cerviniventris* extends to New Guinea without differentiation. The rain forest *Ailuroedus crassirostris*, however, has a range of racial forms in New Guinea.

Clinal variation occurs in the Australian bower-birds in *Sericulus chrysocephalus, Chlamydera maculata, C. cerviniventris*, and *C. nuchalis*.

VIII. THE MECHANISM OF SPECIATION ON THE AUSTRALIAN CONTINENT

The Nature of Geographic Variation in species. Quantitative Treatment

The nature of the variation in the 425 species constituting the sample is summarized on Table 3. Each species is graded according to whether it is monotypic or polytypic. The polytypic species are divided into those with clinal variation only and those with morphologically differentiated isolates, the number of the latter both within and beyond Australia (section to the east of Wallace's Line) being given. Where species are members of superspecies groups, this is stated. The isolates within Australia are subdivided into two groups: those with moderate to marked differentiations and those with slight differentiation. Finally, the number of hybrid zones (if any) is stated for each species.

The species sampled (425) are subdivisible as follows:—

Monotypic species:	188
Polytypic species with	
clinal variation only:	99
with isolates:	138
TOTAL: Polytypic species:	237

In terms of percentages then, it will be seen that 44 per cent of the species sampled (including those that are geographically representative) are monotypic, and 23 per cent have clinal variation only, whilst 33 per cent have isolates in Australia.

The number of morphologically differentiated isolates totals 213-220, averaging 0.5 per species for the fauna as a whole, and 1.6 per species for the 138 that have them. Of the isolates, 59 (27 per cent) have differentiated to a marked or moderate degree, and 154-161 (73 per cent) are but poorly differentiated.

Not included in the calculations are populations, particularly of sclerophyll forest species in Tasmania and the southwest, that are isolated but have not undergone any differentiation. The majority of these either have been isolated too short a time for differentiation to occur or are "conservative" species. Nevertheless, it should be recognised that such forms represent the first stage in the speciation process. Excluding these, it can be said that over 200 forms on the continent are potentially new species. One species, *Pachycephala pectoralis,* has 5 to 7 isolates.

Hybrid zones, indicating isolation that broke down before the differentiating stocks had reached specific level, occur in 30 species.

Examples of Species Formation and Intermediate Stages in the Speciation Process

The review demonstrates that active species formation is not only occurring today in most bird families but in almost every part of the continent. All speciation is spatial (geographic). There is no suggestion that it is occurring anywhere sympatrically (see Section XII).

Reference to Table 3 shows that the number of minor and major isolates in the Australian avifauna is large. Of even greater significance, however, in considering examples of intermediate stages in the speciation process are the many isolates that are now as, or more, different from their parental stocks than (genetically) proven species in their genera. These are the semi-species of Mayr (1942, p. 165). Finally, there are various instances of recently completed speciation, as demonstrated by marginal overlaps without interbreeding.

The families and subfamilies in which the full range of intermediate states in the speciation process occur within Australia are as follows: Accipitridae, Psittacidae, Menuridae, Campephagidae, Muscicapinae, Malurinae, Sittidae, Dicaeidae, Meliphagidae, Cracticidae. Possibly the Columbidae and Ploceidae also come into this category for *Geophaps scripta* and *G. smithi* in the former, and *Poephila acuticauda* and *P. cincta* in the latter, could actually be examples of the final stage in the speciation process, and not just unusually distinctive isolates. Those families that have Australian isolates at all stages of differentiation are: Ardeidae, Atrichornithidae, Timaliinae. In the Turnicidae, Alcedinidae, Silviinae, Zosteropidae, and Oriolidae, there are morphologically differentiated isolates of lesser degree.

Instances of Mayr's "proofs" of geographic speciation, i.e. the existence of superspecies, marginal overlaps, double invasions, and circle formation, occur in Australian birds as follows:—

(a) Superspecies

Almost one-third of Australian bird species belong to superspecies groups (column 6 in Table 4). Depending on the group, these lie mainly outside of, or within, the limits of the continent. In the long view, of course, several of the larger Australian birds are direct counterparts of species occurring in other parts of the world, e.g. the eagle *Aquila audax* is closely related to the Palaearctic Golden Eagle, *Aquila chrysaetos*. (Those species that belong to superspecies groups to the *west* of Wallace's Line have the figures in brackets.) Species belonging to superspecies centered in the island sector to the north of Australia and *east* of Wallace's Line include members of the families Columbidae (e.g., *Macropygia phasianella*), Psittacidae (*Trichoglossus moluccanus*), Alcedinidae (*Halcyon sancta* and *H. chloris*), Campephagidae (*Coracina tenuirostris*), Muscicapinae (*Arses kaupi, Monarcha melanopsis, Heteromyias cinereifrons*), Malurinae (*Gerygone* (*igata*) *richmondi*), Dicaeidae (*Dicaeum hirundinaceum*), Meliphagidae (*Myzomela dibapha, Meliphaga notata*), and Ploceidae (*Erythrura trichroa, Lonchura flaviprymna*).

Many superspecies groups are confined to the Australian continent. These include those in the following families and genera: Columbidae (*Geophaps*), Psittacidae (*Platycercus, Barnardius, Psephotus,* and *Neophema*), Muscicapinae (*Petroica*), Malurinae (*Gerygone, Sericornis, Amytornis, Stipiturus,* and *Malurus*), Sittidae (*Climacteris*), Dicaeidae (*Pardalotus*), Meliphagidae (*Melithreptus, Acanthorhynchus, Meliphaga, Anthochaera*), Ploceidae (*Zonaeginthus, Poephila*), and Cracticidae (*Gymnorhina, Strepera*).

(b) Marginal overlap of Recently Evolved Species

Some examples of this are as follows:—

Psittacidae: Neophema elegans, N. chrysostoma, and *N. chrysogaster,* overlap in parts of Victoria and South Australia. Areas of maximum concentration today suggest that *N. elegans* has arrived, secondarily, from the west, and *N. chrysogaster* from Tasmania.

Campephagidae: Coracina robustus and *C. papuensis* co-exist in the Cairns-Atherton area of Queensland, the latter presumably being the more recent arrival.

Muscicapinae: Petroica rosea and *P. rodinogaster* now breed together in southern Victoria. The latter developed in Tasmania.

Pachycephala rufogularis and *P. inornata* overlap in the mallee of Victoria, the latter apparently being a secondary invader from the west of the continent (Fig. 13).

Malurinae: Amytornis textilis and *A. modestus* both breed in the Macdonnell Ranges, the former having colonized the area from the west, and the latter from the east (Fig. 17a).

Hylacola cauta (western) and *H. pyrrhopygia* (eastern) now overlap distributionally in the Bendigo area of Victoria.

Sittidae: Climacteris picumnis (*melanota*) and *C. melanura* co-exist at the head of the Gulf of Carpentaria, the latter being an invader from the west (Fig. 22).

Dicaeidae: Pardalotus substriatus and *P. melanocephalus* live together in coastal eastern Queensland, the latter obviously being an invader from the north of the continent.

Meliphagidae: Melithreptus lunatus and *M. albogularis* occupy the same spatial relationship to each other as do *Pardalotus* but in this case the overlap zone extends for several hundred miles (Fig. 23). *Myzantha melanotis* and *M. flavigula* occupy adjacent zones in the Victorian mallee area, the former apparently being an "old" mallee form and the latter the recent invader.

Cracticidae: Cracticus torquatus and *C. mentalis* co-exist in Cape York, the latter possibly being a recent colonizer from New Guinea.

The co-existence of *Menura novae-hollandiae* and *M. alberti* in adjacent areas in northeastern New South Wales and southern Queensland is also an instance of range junction or overlap between related species though, in this case, obviously not a very recent one.

(c) Double Invasions

These, of course, are special cases of range overlap. They occur in two main areas: northern Australia, and Tasmania. There are also one or two apparent instances in southwestern Australia.

Entry into the Australian continent is only possible at a couple of points: through Cape York and, to a lesser degree, through the northwest corner. Tropical invaders can mostly only colonize down the coastal rain forest and monsoon forest tracts. This enables a fairly clear picture to be gained of the significance of double invasion in the speciation of Australian birds.

Colonization of northern Australia from the New Guinea-Timor segment:

(i) *Meliphaga lewini, M. notata,* and *M. gracilis* (honeyeaters). These three rain forest species now co-exist in the Cairns-Atherton area and represent successive waves of, and degrees of differentiation from, the ancestral stocks in New Guinea (Fig. 24).

(ii) *Philemon argenticeps* and *P. novaeguineae* (honeyeaters). In this case *P. argenticeps,* extending widely over the north of the continent, represents the first wave of colonization. Subsequent waves have independently entered Cape York (*P. novaeguineae yorki*) and Arnhem Land (*P. novaeguineae gordoni*) (Fig. 26).

(iii) *Coracina robusta* and *C. papuensis* (cuckoo-shrikes) are examples of an "old" Australian species (but whose ancestors must have entered from the tropics) being secondarily contacted, in the north of its range, by a later invader.

(iv) The two species of teal ducks (*Anas castanea* and *A. gibberifrons*), and the hovering kites (*Elanus scriptus* and *E. notatus*), represent somewhat older cases of speciation by double invasion. They now co-exist over a broad area.

(v) *Arses kaupi* and *A. telescophthalmus lorealis* (flycatchers) and *Meliphaga macleayi* and *M. chrysotis* (honeyeaters). In these cases the earlier and later arrivals, though isolated from each other in the Cairns-Atherton and Cape York sections, respectively, are so distinct that they must be genetic species.

(vi) Various infraspecific forms. "Simultaneous" invasion of Arnhem Land and Cape York by different races, which remain isolated in Australia, can be seen in *Butorides striatus, Myzomela erythrocephala,* and others. In a few cases a second wave of colonization by a stock, entering the continent at a common point, now hybridizes with the earlier one. In *Accipiter fasciatus* such hybridization occurs over a broad front. In a few species, the later invader has not yet contacted the earlier one. *Monarcha trivirgata* is an example of this, the New Guinea race occupying Cape York and the Australian one the country to the south of the Princess Charlotte Bay dry barrier, as in "(v)" above.

Colonization of Tasmania from Australia:

(i) *Acanthiza ewingi* and *A. pusilla* (Malurinae). In this case *A. ewingi* represents the derivatives of the earlier wave and *A. pusilla* (race *diemenensis*) the later one.

(ii) *Pardalotus quadragintus* and *P. punctatus* (Dicaeidae). This is a parallel case, with *P. quadragintus* the earlier element.

(iii) The two insular "species" of *Strepera* (*arguta* and *fuliginosa*) could represent a double invasion of the island by one or the other of the mainland species, i.e. either *S. versicolor* or *S. graculina.* Most workers feel, however, that a representative of each is involved.

Colonization of the sclerophyll forests of the southwest corner of the continent from the southeast:

Double invasion of the isolated pocket of sclerophyll forest in southwestern Australia by the robin genus *Eopsaltria* would appear to be the explanation for the occurrence there of two species, *E. georgiana* (representing the descendents of the earlier wave) and *E. australis* (*griseogularis*). Speciation in the *Malurus lamberti* complex could be accounted for by at least one of the species advancing from the east around the head of the Great Australian Bight.

(d) Speciation by Circle Formation

The only real instance of this in Australia is in the parrot *Platycercus elegans* (Fig. 11).

The honeyeater, *Meliphaga versicolor*, in that it developed its differences in New Guinea and from there has reinvaded Australia to occupy zones adjacent to its near relatives *M. virescens* and *M. fasciogularis*, presents, to a degree, a parallel in the north of the continent (Fig. 25). The white-breasted races of the finch, *Neochmia phaeton*, have had a similar origin.

Classificatory Position and Speciation

As will be seen from Table 4, summarizing the results in terms of families, there is a considerable amount of variation in the "speciation potential" of the different bird groups.

The hawks have only about 3 isolates in Australia and they are poorly differentiated ones. The larger water birds (grebes, herons and ducks) demonstrate similarly weak tendencies. In the case of the herons only 5 isolates are developed in Australia.

The ducks have no continental isolates though several occur in the Rallidae.

Large water birds have a very slow evolutionary rate, Howard (1946) having shown that many of them have not changed skeletally since the Miocene.

The pigeons (Columbidae), inhabiting a wide range of habitat types, have 10-11 isolates in Australia and, since they total 22 species, approximately reflect the average for the avifauna as a whole (0.5 isolates per species). The parrots (Psittacidae), equally diverse in habitat requirements, have 17-18 isolates in 33 species. Many of the species in this family, are, however, geographically representative. The ratio of isolates to species in the kingfishers (Alcedinidae) is 4 to 10.

In the cuckoo-shrikes (Campephagidae) there are 7 isolates in 8 species (1.0 per species). This is a figure typical of many of the small passerine groups, e.g. Malurinae with 61-62 isolates in 69 species, and the Muscicapinae with their 33-35 isolates in 43 species. The latter groups, it should be noted, are largely composed of sedentary species.

The Meliphagidae have 18 isolates in 67 species, although here again there are a number of geographically representative species. The Estrildinae, most of which are restricted to the north, have 6 isolates in 18 species. The Artamidae, which have continuous ranges and are nomadic, have no isolates in 6 species.

The endemic Australian Cracticidae, all of which are relatively large birds, have 11-12 isolates in 11 species. In this case, however, 4 of the latter are actually of uncertain genetic status so that the actual figure may be 1.5 isolates per species.

The family to which a species belongs can be seen to influence its potential for giving rise to new species not through any innate genetic characteristic so much as through what might be described as its ''ecological attributes.'' Included in these are body size and general mobility (large birds require a larger foraging area than small ones), nature of seasonal movements, type of food ''niche'' occupied, and habitat. Small insectivorous birds commonly live in a habitat that is specialized and restricted, and have poor dispersive capabilities.

The influence of the ''history'' of a group on speciation patterns is seen in the interesting differences between the flycatcher subfamilies Muscicapinae and Malurinae. The bulk of the genera in the latter are true endemics and speciation is taking place almost wholly *within* the continent. The Muscicapinae, however, whilst they do contain endemic genera, are best developed in the tropics and most of the isolation and speciation is taking place either outside of Australia or between New Guinea and Australia.

Habitat Specificity and Speciation

As noted, the majority of Australian bird species are restricted to, or reach the peak of their abundance, in one or another of the basic vegetation formations. Thus, as will be seen from Table 2, 16 per cent are rain forest dwellers, 16 per cent live in sclerophyll forest, 2 per cent in mallee, 4.5 per cent in mulga, 3 per cent in desert (spinifex) grassland, 3 per cent in mangroves, 14 per cent in swamps and marshes, and so on. The remainder are less specific but nevertheless are oriented to one or the other of the "intermediate-type" habitats of savannah woodland (28 per cent) and savannah grassland (11.5 per cent).

That the habitat category into which a species falls has an important influence on its potential for developing isolates and hence undergoing speciation will be seen from Tables 5 and 6. Thus the 70 rain forest species sampled have 31 morphologically differentiated isolates (0.5 per species). In addition to some recently developed geographically representative species (in Tasmania and southwestern Australia) the 80 sclerophyll forest species have 71-72 isolates (1.0 per species). The 113 savannah woodland species have 61-64 isolates (0.5 per species), the 44 savannah grassland species 10 isolates (0.2 per species). Ten mallee species have 4 isolates (0.4 per species). Fifteen mulga species have no isolates. Fifteen desert grassland (spinifex) species have 8 isolates (0.5 per species), 16 mangrove species, 10-11 (0.6 per species), and 54 swamp species only 11-12 (0.2 per species). The 9 species placed in the miscellaneous habitat category (e.g., *Lophophaps plumifera, Epthianura crocea*) have 7-8 isolates (0.8 per species).

If the figures be expressed as percentages (Table 6) it will be seen that of the total isolates about 14 per cent are rain forest forms, 33 per cent are sclerophyll forest birds, 30 per cent belong to savannah woodland, 5 per cent to savannah grassland, 2 per cent to mallee, nil to mulga, 4 per cent to desert grassland (spinifex), 5 per cent to mangroves, 5 per cent to swamps and marshes, and 3 per cent to miscellaneous habitats.

One of the significant facts revealed by Table 6 is that the bulk of the morphologically differentiated isolates or "incipient species" in Australia are coming from species that are predominantly inhabitants of sclerophyll forest and savannah woodland. These account for 33 per cent and 30 per cent, respectively, a total of 63 per cent of all isolates. In contrast with the tropical rain forest and mangrove habitats (that are mostly restricted to the northern fringe of the continent) these are "true Australian" vegetation formations. They have the combination of being extensive, biotically rich, and yet are broken up into several isolated tracts. In these regards they contrast with the dry-country vegetation formations, the savannah grassland, mulga, mallee, and spinifex, and with the swamp-river habitat.

The highest proportion of isolates that can be described as well differentiated, as compared to slightly differentiated, occur in savannah woodland (32 per cent), sclerophyll forest (25 per cent), and rain forest (22 per cent), respectively.

Hybrid zones are most numerous amongst the inhabitants of the savannah woodland, sclerophyll forest, and savannah grassland habitats, accounting for 54 per cent, 24 per cent, and 18 per cent of the figures, respectively. The savannah areas, occupying "intermediate" climatic zones are presumably the most sensitive and responsive to minor climatic shifts. Sclerophyll forest and savannah woodland have, more than any other associations, been subject to alteration by human settlement.

Species in which the only variation is of a clinal nature are most numerous in savannah woodland (43 per cent), sclerophyll forest (14 per cent), and savannah grassland (16 per cent).

Species that do not vary geographically are also most numerous in savannah woodland (many of the inhabitants of which are nomads, with others restricted either to the north or south), swamps (most inhabitants nomadic), rain forest (most are New Guinea immigrants restricted to the far north), and sclerophyll forest (many restricted to part of the southeast or Tasmania).

Species with isolates beyond Australia belong mainly to four habitat categories in Australia: mangroves, rain forest, sclerophyll forest and savannah woodland. In the case of the first two of these, this is to be expected as these vegetation formations have a wide distribution through the tropics. That so many sclerophyll and savannah woodland birds are involved might seem strange. The explanation is that the species concerned are those that already exhibit a fairly wide degree of habitat and ecological versatility in Australia, so that adjustment to a new habitat in the islands apparently presents no problem. Examples, and the number of isolates beyond Australia, are: the hawks (*Aviceda subcristata* (12), *Accipiter novaehollandiae* (19), *A. fasciatus* (6); the cuckoo-shrikes *Coracina papuensis* (9) and *C. tenuirostris* (18); the whistler *Pachycephala pectoralis* (51); the wood-swallow *Artamus leucorhynchus* (7); the dove *Geopelia striata* (3); the honeyeater *Philemon novaeguineae* (8); and the white-eye *Zosterops lateralis* (6). The rain forest *Rhipidura rufifrons*, by contrast, is an example of a species with a restricted habitat tolerance in Australia but that exhibits ecological versatility in the southwest Pacific where a number of diverse islands are occupied.

Seasonal Movements and Speciation

The influence of seasonal movements on isolation and speciation is summarized in Table 7. Two-thirds of the sedentary and migratory species vary geographically. Only one-quarter of the nomads, however, do so. Almost all of the isolates, as well as the hybrid zones, occur in the sedentary species. The number of morphologically differentiated isolates and the number of isolates per species for the three categories is as follows:

	Number of Morphologically differentiated isolates in Australia	Number of isolates per species
Sedentary species 294 (69%)	191-196	0.65
South-north migrants 32 (8%)	15-17	0.50
Nomads 99 (23%)	7	0.07

It will be seen that the nomadic way of life virtually eliminates any chance of isolation and speciation developing. This is brought out in equally striking fashion by the individual bird groups. The hawks and large water-birds are mostly nomads. Within the parrot family the nomadic *Melopsittacus* (Fig. 9) and *Leptolaimus* do not vary, whereas most genera composed of species that are essentially sedentary or resident, like *Psophotus* and *Platycercus*, have many isolates. Parallel cases are the nomadic *Certhionyx* and *Granticlla* amongst the honeyeaters, as compared to most members of *Meliphaga*. *Epthianura*, amongst the Malurinae, and *Artamus*, in the Artamidae have, on the one hand, sedentary species that show geographic variation and, on the other, nomadic species that do not show any at all.

South-north migration, by contrast, does not preclude the development of geographic variation and isolation, in part because many of these undertake seasonal movements over part of the range only, e.g. *Zosterops lateralis* and *Gerygone olivacea*. The relationship between variation and south-north migration in the campephagids *Coracina novaehollandiae* and *C. tenuirostris* has already been discussed. A reasonable inference with respect to most true south-north migrants in Australia is that, since they tend to inhabit the fertile coastal strip, they are able to return to the same areas to breed from year to year. This contrasts with the situation in nomads like *Epthianura tricolor* and *Lalage tricolor* which, though there is a south-north component to the movements, concentrate for breeding where seasonal conditions are maximal.

IX. GEOGRAPHIC ISOLATION

An understanding of the barriers initiating speciation in Australian birds necessitates a detailed review of the distribution of the major vegetation formations in the light of those bird species living in them.

Terrestrial Isolating Barriers

(a) Rain Forest

Rain forests are confined to the eastern seaboard and are broken up into a series of tracts and pockets (Fig. 5). There are, however, three main areas: (i) Cape York, (ii) Cairns-Atherton, (iii) and South Queensland-northern New South Wales. Each of these has some striking ornithological elements, the Cairns-Atherton section being particularly rich in this respect.

(i) *The Cape York rain forest tract:* These forests are chiefly of significance in that many New Guinea species have recently colonized the northern section. There are some 15 of these species, most undifferentiated: *Amaurornis olivaceus*, *Probosciger aterrimus*, *Larius roratus*, *Geoffroyus geoffroyi*, *Syma torotoro*, *Podargus ocellatus*, *Cacomantis castaneiventris*, *Drymodes superciliosus* (also on Roper River), *Microeca grisciceps*, *Tregellasia leucops*, *Monarcha frater*, *Sericornis beccarii*, *Craspedophora magnifica*, *Glycichaera fallax* and *Meliphaga chrysotis*. In several polytypic rain forest species the Cape York form represents a recent, independent wave of colonization from New Guinea, e.g. *Megaloprepia magnifica*.

The only species endemic to the Cape York rain forests is the honeyeater *Trichodere cockerelli*. There are, however, several distinctive races that have differentiated there, e.g. *Arses telescophthalmus lorealis*.

Ornithological data suggests that the Cape York rain forests have had the following history. They figured as "bridges" in earlier waves of colonization of the Cairns-Atherton forests by New Guinea species, but subsequently became reduced to such an extent that they could no longer support some of these forms. They have recently expanded again, but not to their former extent. The evidence for this is that a couple of genera, and species, requiring dense rain forest conditions, occur in New Guinea and in the Cairns-Atherton area, but not now in the intervening Cape York rain forests, e.g. the robin *Heteromyias*, the log-runner *Orthonyx* and, apparently, the swiftlet *Collocalia spodiopygia*. Again, the endemic bower-bird, *Prionodura newtoniana*, has New Guinea affinities. It is presumed that these forms became secondarily exterminated from the Cape York area. Tate (1952) finds similar distributional anomalies in the mammals of northeastern Australia, and feels too that these can only be explained in the above manner. An interesting alternative suggestion is, however, advanced. This is that, when Torres Strait was dry land and the climate was wetter, the confluence of the rivers flowing southwards from Papua must have approached that of the Australian ones flowing northwards across the Gulf of Carpentaria. The accompanying riverside forests would conceivably have provided a migration route from New Guinea to Atherton that by-passed Cape York.

As noted, there is currently much colonization of northern Cape York by New Guinea species suggesting re-establishment, or expansion, of this habitat.

(ii) *The Cairns-Atherton rain forests:* These are quite extensive and, in terms of the number of species endemic to them, are of considerable significance. There are some 8 such species: *Heteromyias cinereifrons*, *Colluricincla boweri*, *Arses kaupi*, *Oreoscopus gutturalis*, *Meliphaga frenata*. and *M. macleayana*, *Prionodura newtoniana* and *Scenopoeetes dentirostris* (both bower-birds). Some 25 rain forest and sclerophyll forest species have isolates of infraspecific rank here. They include *Acanthorhynchus tenuirostris, Ninox novae-seelandiae, Climacteris leucophaea, Eopsaltria capito, Pachycephala pectoralis, Gerygone (igata) richmondi, Acanthiza nana, Acanthiza pusilla,* and *Opopsitta diophthalma.*

There can be no doubt that the elevated and dissected Atherton area is a "refuge" of long standing. The rainfall today exceeds 80 inches per annum and in one small section reaches 160 inches per annum. It is probable that even in the event of a marked reduction in overall continental rainfall this sector would still be covered with rain forest.

(iii) *The southern rain forest tracts:* These extend from about the Bunya Mountains in southern Queensland to Dorrigo in central New South Wales. Thereafter they taper out as a series of small pockets. They are most dense and extensive in the Lamington area on the Queensland-New South Wales border.

Only between one-third and one-half of the true rain forest species extend south to this last sector. Within the 400-500 miles of the tract, moreover, there is a steady falling off in the number of species. A few, however, extend right through to the restricted, cold, subtemperate rain forests in the Dandenongs in Victoria, e.g. *Meliphaga lewini.*

Amongst the species endemic to the southern rain forests and associated wet sclerophylls are the bower-bird *Sericulus chrysocephalus,* the scrub-bird *Atrichornis rufescens* and the frogmouth *Podargus (ocellatus) plumiferus.* A lyrebird species, *Menura alberti,* is confined to the elevated Lamington segment in the north, where there is also a race of the southern sclerophyll whistler, *Pachycephala olivacea (macphersiona).*

(iv) *Barriers and Speciation:* Speciation occurs mainly between the three major tracts. The two commonest patterns are for the Cairns-Atherton and southern tracts to be occupied by distinctive isolates and for the Cape York and Cairns-Atherton tracts to be populated by forms that have reached a lesser degree of divergence. Examples are:—

Species with a distinctive isolate in each of the three main tracts: *Opopsitta diophthalma* (see Fig. 10), *Megaloprepia magnifica, Tregellasia capito-leucops.*

Species with distinctive isolates in the Cairns-Atherton and southern tracts only: *Ptilonorhynchus violaceus, Ailuroedus crassirostris, Sericornis citreogularis,* and *S. magnirostris. Gerygone* (*igata*) *richmondi* has, in addition, an isolate in the Bowen-Mackay tract.

Species with isolates in the Cape York and Cairns tracts only: *Machaerirhynchus flaviventer, Meliphaga analoga* and *M. gracilis*. In the flycatcher *Arses* the two tracts are populated by separate species. The warbler *Gerygone palpebrosa* has, in addition, a third isolate in the Mackay-Rockhampton section.

The barriers breaking up rain forest tracts in Australia, and hence the distribution of rain forest species, have been listed by Tate (1952). They are areas of dry savannah, as follows:—Coen-Cooktown gap (southern Cape York), width 150 miles; Burdekin gap (Townsville-Bowen), 125 miles; Mackay-Rockhampton gap, possibly less complete, about 150 miles; Rockhampton-Miriamvale gap (near Bundaberg), 100 miles; Toowoomba-Brisbane gap, 75 miles. A number of the bird species appear to be absent from the whole section between about Mount Spec, near Townsville, and the Bunya Mountains. In the case of these, the effective distributional barrier is some 400 miles wide. This is almost three times the distance between the Cairns-Atherton and Cape York tracts and explains the greater differentiation of many southern forms.

It is obvious that the distribution of rain forest bird species in Australia today can only be explained in terms of greater continuity of this habitat in the past. In particular, the "pockets" between the Cairns area and the Bunya Mountains must formerly have been larger and more extensive.

(b) Monsoon Forest

Monsoon forests or pseudo-rain forests form narrow strips along many of the coastal rivers in the dryer north and northwest of the continent, an area of summer monsoon rainfall. Superficially, they resemble rain forests but differ in their restricted extent and relative dryness.

Monsoon forests, and the denser mangrove areas that are frequently adjacent to them, enable a number of eastern rain forest species to occur in the Northern Territory. There are about 12 of these and, with the exception of only two or three (e.g. *Chibia bracteata, Gerygone magnirostris*), all are represented by distinctive northwestern isolates. Such species are: *Rhipidura rufifrons, Piezorhynchus alecto, Drymodes superciliosa* and *Poecilodryas superciliosa, Lalage leucomela, Ptilinopus regina* and *Chalcophaps indica, Myzomela obscura* and *M. erythrocephala*.

Only a couple of species of birds are restricted to the monsoon forests of the Northern Territory. These species, *Gerygone chloronota* and *Ptilinopus* (*cincta*) *alligator*, have colonized the continent from western New Guinea and the Sumba Islands, respectively.

The barrier separating the Arnhem Land and eastern populations of rain forest species is the Gulf of Carpentaria and the dry country at its head, commonly leading to a range gap of 400-500 miles. The northwestern form of the rain forest flycatcher *Rhipidura rufifrons*, however, secondarily extends as far east as western Cape York.

(c) Sclerophyll Forest

The Australian sclerophyll forests are broken up into four sections, three of which are extensive (Fig. 5). These are: (i) The southeastern section extending from north of the Bunya Mountains to the southeastern corner of South Australia (about 1,300 miles), and typically bordered by the sea and Great Divide. (ii) Tasmania, insular, about 170 miles from north to south and slightly less from east to west, mostly sclerophyll. (iii) Southwest corner of the continent, a triangular section with a length of some 150 miles and a depth of 60 miles. (iv) The Mount Lofty Ranges and Kangaroo Island, two small, adjacent sections each measuring perhaps 100 by 20 miles.

In the east of the continent, various species that are basically sclerophyll inhabitants extend through the wetter coastal savannahs of eastern Queensland well beyond the limits of the sclerophyll forests proper. Again, in New South Wales, some extend a short distance inland through the denser riverside savannahs of the Murrumbidgee, Lachlan, and Murray, or into elevated sections to the west of the main range (Warrumbungle Mountains and Grampians).

The avifaunas of the four main sclerophyll areas may be summarized as follows:

(i) *Southeastern sector:* The main sclerophyll fauna is here. Almost all southwestern and Tasmanian sclerophyll forms have exact counterparts in the southeast, but the southeastern tract has various endemic forms absent from the others. The species restricted to the area include: *Menura novaehollandiae*, *Alectura lathami*, *Pycnoptilus floccosus*, *Cinclosoma punctatum*, *Callocephalon fimbriatum*, *Dacelo novaeguineae*, *Acanthiza lineata*, *Petroica rosea*, *Eurostopodus mysticalis*, *Meliphaga melanops*, *Manorina melanophrys.* The various nectar-feeding lorikeets, confined to the east, can equally be regarded as sclerophyll forest or savannah woodland forms.

(ii) *Southwest:* Two species only are unique to this area. These are the parrot *Purpureicephalus spurius,* whose nearest relative is believed to be a New Caledonian species, and the robin *Eopsaltria georgiana.* The latter probably represents the descendents of the first of two waves of colonization by the genus. Two wrens, *Malurus pulcherrimus* and *M. elegans*, are now known to be genetic species, though their counterparts in the east are infraspecific. An additional 10 forms, though isolated from their eastern relatives, are so distinct morphologically that they must have, or probably have, reached specific distinctness: *Calyptorhynchus baudini, Atrichornis clamosus, Sericornis maculatus* (extending into South Australia), *Malurus splendens, Neophema petrophyla, Platycercus icterotis, Climactoris rufa, Zonaeginthus oculatus, Gymnorhina dorsalis* and *Acanthorhynchus superciliosus.*

There are some 20 lesser isolates, most of them differentiated to only a minor extent. Perhaps 10 sclerophyll forest species have undifferentiated isolates in the southwest.

Southwestern Australia is remarkably rich floristically. For discussion of the flora, distribution maps of the various vegetation formations and factors delimiting them, see Gardner (1944; 1959).

(iii) *Tasmania:* The avifauna of this tract has a similar relationship to the continental southeast as does that of the southwest. There is one endemic genus, the monotypic *Acanthornis*, a small warbler-like bird. There are three proven genetic species: *Acanthiza ewingi, Pardalotus quadragintus,* and *Petroica rodinogaster. Lathamus discolor, Neophema chrysogaster,* and *Pardalotus striatus,* also occurring on the mainland, apparently originated in Tasmania. About 12 endemic Tasmanian forms are still isolated from their mainland relatives but exceed, or equal, the degree of differentiation typical of species: *Tribonyx mortieri, Platycercus caledonicus, Sericornis humilis, Petroica vittata, Meliphaga flavicollis, Anthochaera paradoxa, Melithreptus affinis, M.* (*gularis*) *validirostris, Strepera fuliginosa* and *S. arguta* (the last three the least distinct).

Twenty or so of the mainland sclerophyll species have isolates on Tasmania that have attained a slight to moderate degree of distinctness, whilst perhaps a dozen are represented by undifferentiated populations.

(iv) *Mount Lofty Ranges and Kangaroo Island:* This area is merely an outlyer of the southeastern tract. Various species do not, however, extend through to here.

In about 10 species, the populations isolated here have undergone a minor amount of differentiation, e.g. *Phylidonyris pyrrhoptera, P. novaehollandiae, Acanthorhynchus tenuirostris, Zosterops lateralis, Stipiturus malachurus, Acanthiza lineata, A. nana, A. pusilla, Strepera versicolor, Climacteris leucophaea.* Gene flow has been resumed with the east in *Zosterops lateralis* and *Pachycephala pectoralis*, presumably as a result of a minor amelioration in climatic conditions. In a few instances the Kangaroo Island populations have differentiated to a minor extent from the Mount Lofty ones (see Table 8).

(v) *Barriers and Speciation:* Variation and speciation in the sclerophyll forest species follow a clear-cut pattern. They are typically broken up into three to four stocks. In a couple of instances there are differentiated populations in each of the tracts, e.g. *Acanthorhynchus tenuirostris, Zosterops lateralis.* The important trends, however, occur between Tasmania, the southwest, and southeast.

Species with distinctive isolates both in Tasmania and in the southwest: *Gymnorhina tibicen* supersp., *Platycercus eximius* supersp., *Anthochaera carunculata* supersp., *Rhipidura fuliginosa, Melithreptus lunatus* supersp., *Phylidonyris novae-hollandiae, Pardalotus punctatus* supersp., *Acanthiza pusilla, Sericornis frontalis* supersp., *Strepera versicolor., Malurus cyaneus-splendens* group, *Calamanthus fuliginosus, Stipiturus malachurus, Pachycephala pectoralis, Turnix varia.*

Species with distinctive isolates in the southwest only, i.e. in which the Tasmanian stock (when present) has not differentiated: *Zonaeginthus bellus, Petroica multicolor.* The following do not occur in Tasmania: *Eopsaltria australis, Phylidonyris niger, Dasyornis brachypterus* and *D. broadbenti.*

Species in which the Tasmanian stock alone has differentiated: *Phylidonyris pyrrhoptera, Platycercus elegans* supersp., neither of which occur in the southwest; *Meliphaga leucotis* supersp; *Aquila audax*, with a wide range over Australia, has a minor form in Tasmania.

The four sections are isolated from each other by the following barriers:—

Bass Strait. This has a width of 100 miles but intervening islands reduce the maximum water gap to 50 miles.

Coorong arid tract, southeastern South Australia. This 90-100 mile wide section of sand and sparse scrub isolates the Mount Lofty Ranges.

Spencer Gulf. This deep coastal indentation is some 50 miles wide at the mouth.

Nullarbor Plain and the Great Australian Bight. A vast tract of sparse and stunted desert vegetation, 500 miles wide, stretches westwards from Eyre Peninsula. It is this and Spencer Gulf that isolate the sclerophyll forest of the southwest corner. (see also page 439.)

There can be no doubt that the sclerophyll forests of southeastern and southwestern Australia must at one time have extended much closer to each other, or else that a tongue of "damp scrub" suitable as a bird habitat, joined them. Isolation resulted from, in all probability, post-Pleistocene climatic and sea-level changes. To what extent the arid Nullarbor barrier would have to be narrowed to permit an interchange of sclerophyll birds between east and west cannot be stated. Some species are better adapted to dry conditions than others, as seen from the varying distances between eastern and western populations in different species (note Fig. 6 in Serventy and Whittell, 1951). On the other hand, the 90-100 mile wide Coorong arid barrier is completely effective in a large number of species.

It is interesting to note that a couple of the sclerophyll forest species that occur both in the east and the southwest are absent from the Mount Lofty-Kangaroo Island section, e.g. *Eopsaltria australis*, *Phylidonyris niger*, despite the occurrence of suitable habitat. This suggests that there has been secondary extinction in the region. On the other hand, a couple of southwestern forms have secondarily crossed the Nullabor Plain to occur in the savannah woodlands of Eyre Peninsula.

(d) Savannah Woodland

Whilst many savannah woodland species occur throughout the range of the association there are distinct northwestern and southeastern components. The former is richer. These could be said to inhabit the "tropical" and "temperate" section of the woodlands, respectively, although no real dividing line exists between them.

The vegetation maps show savannah woodland as extending in a broad belt through the eastern and northern sections of the continent (Fig. 5) but bird studies demonstrate that there is a major severance of the fauna into northwestern (Arnhem Land) and eastern components. There is, in addition, a minor differentiation in the case of a few species as between Cape York and the woodlands farther south. An extensive tract of country in the Hamersley section of Western Australia, shown on the map as savannah grassland but containing various (predominently) savannah woodland bird species, and the isolated desert mountain ranges of central Australia, can also best be considered here. Melville Island, lying some 20 miles off Arnhem Land, has a few minor isolates. The restricted section of savannah woodland in southwestern Australia is of no significance ornithologically.

(i) *Kimberleys and coastal Northern Territory:* This tract contains many endemic elements, whilst others characteristic of the northern coastal fringe as a whole obviously originated here. Northwestern species without counterparts in the northeast include the rock pigeons *Petrophassa albipennis* and *P. rufipennis*, the finches *Lonchura pectoralis* and *L. flaviprymna*, and the honeyeater *Meliphaga albilineata*. Northwestern species with counterparts in the northeast are listed below.

(ii) *Cape York and northeastern Australia:* This section is populated by virtually the same species, or their counterparts, as the previous one. In a few instances, however, it has been invaded by additional savannah species from New Guinea, e.g. the friarbird *Philemon novaeguineae* (*yorki*) and the white breasted race (*albiventer*) of the finch *Poephila phaeton*.

Speciation is actively occurring as between the northwest and northeast of the continent in savannah woodland birds:

Northeastern Form	Northwestern Counterpart
Proven Species (contact without interbreeding)	
Climacteris picumnus melanota	*Climacteris melanura*
Isolated forms that have obviously reached that stage of differentiation typical of species.	
Geophaps smithii	*Geophaps scripta*
Platycercus adscitus	*Platycercus venustus*
Poephila cincta	*Poephila acuticauda*
Malurus dulcei	*Malurus amabilis*
Well differentiated isolates	
Psephotus c. chrysopterygius	*P. c. dissimilis*
Poephila personata leucotis	*Poephila p. belcheri*
Lesser Isolates	
Entomyzon c. cyanotis and *E. c. hedleyi*	*Entomyzon cyanotis albipennis*
Halcyon m. macleayi	*Halcyon m. publa*
Neositta chrysoptera leucocephala and *N. c. striata*	*Neositta chrysoptera leucoptera*
Myzomela erythrocephala kempi	*Myzomela erythrocephala*

In addition to the above, it is probable that the honeyeater *Melithreptus albogularis*, and possibly *Pardalotus melanocephalus*, developed in northwestern Australia and are secondary inhabitants of eastern Australia (Fig. 23).

(iii) *Eastern Australia:* Included in the savannah woodland inhabitants restricted to (south) eastern Australia are *Pedionomus torquatus* (plain wanderer), the honeyeaters *Meliphaga fusca* and *Plectorhyncha lanceolata*, and the finches *Lonchura modesta* and *Zonaeginthus guttatus*. Most of these are distributed north to about 18 or 20-degree line of latitude, i.e. they do not occur on Cape York.

Evidence of the (former) severance of Cape York and southeastern savannah woodland species is seen from the existence of distinct northern and southern forms in the tree-creeper *C. picumnus melanota* and *C. p. picumnus* (Fig. 22), the fly-catcher *Seisura inquieta* (Fig. 15), and the kingfisher *Dacelo novaeguineae*. In these species the two forms are apparently still isolated. The finch *Poephila cincta*, however, has a hybrid zone at the base of Cape York.

(iv) *Hamersley section of midwestern Australia:* A number of species have distinctive isolates in this section. Amongst these are *Coracina novaehollandiae, Pomatostomus temporalis, Dacelo leachii, Geopelia striata, G. humeralis, Ocyphaps lophotes,* now with a somewhat expanded range, and *Climacteris melanura. Lophophaps plumifera* has a distinctive form (*ferruginea*) amongst the rocky outcrops of the area.

The range of typical savannah woodland forms in this section (*Climacteris melanura wellsi*) will be seen in Figure 22.

(v) *The mountains of central Australia:* The desert mountains constitute a refuge and relict area for some plant and some invertebrate species, populations of which are isolated there hundreds of miles away from their nearest relatives on the coast (Keast, 1959d). Their existence is interesting evidence of a formerly higher rainfall in central Australia. At the vertebrate level, the desert mountains are chiefly of significance in permitting a number of species to live in the interior of the continent that would otherwise be unable to do so.

Two savannah bird species have distinct isolates in the central mountains: *Rhipidura fuliginosa*, in the Levi Range, and *Strepera versicolor*, in the Everard Range.

(vi) *Melville Island:* Some 6-8 Arnhem Land forms have minor isolates on this island (see Table 8).

(vii) *Barriers:* There can be no doubt that the barrier isolating northwestern and eastern savannah woodland components is the tongue of dry country extending through the centre of the continent to the head of the Gulf of Carpentaria. The 30-inch rainfall isohyet reaches the sea here (Fig. 4). A better appreciation can, however, be gained from the climatological map (Fig. 4a), humid and sub-humid zones being isolated by an extensive tract of semi-arid country. A minor fall in sea-level would materially reduce the size of the Gulf.

Differentiation as between Cape York and eastern savannah woodland species has probably taken place on either side of the tongue of dry country (shown on rainfall but not vegetation maps) extending through to the sea in the general Townsville-Burdekin River area (Fig. 4). This was probably more effective previously.

The barrier cutting off the Hamersley section from the north is the tract of the Great Sandy Desert that reaches the sea in northwestern Australia in the vicinity of Eighty Mile Beach, a barrier perhaps 80-100 miles wide. Another arid tract, covered mainly by mulga scrub, extends through to the sea in the general vicinity of Shark Bay. Though vegetated, this effectively keeps the advance elements of southwardly-colonizing savannah and grassland species of the Kimberleys from reaching southwestern Australia.

The mountains of central Australia are surrounded by extensive tracts of arid sand-plain desert.

(e) Savannah Grassland

The ground-feeding grassland species and aerial feeders that require flat plain with scattered trees for perching are either confined to this habitat or reach their peak of abundance here. These include several quail species, the chats *Epthianura tricolor* and *E. aurifrons* (the latter mainly an inhabitant of saltbush within the savannah), a couple of species of *Malurus*, and the cuckoo-shrike *Pteropodocys maximus*.

Savannah grasslands cover extensive areas of Australia. Their borders are sometimes poorly defined, there is interdigitation with other associations and, within the area defined as grassland on the map, there are enclosed tracts and areas of savannah woodland, mulga and saltbush. Their continuous nature and the fact that a high proportion of the avifauna is nomadic explains the virtual absence of isolation and speciation in the bird inhabitants of this habitat.

Barriers: Nil.

(f) Mulga

Many bird species inhabit mulga and adjacent associations (especially savannah grassland) to an equal degree. Only a few species are confined to mulga so that the habitat is of limited significance ornithologically. These include, however, the honeyeater *Conopophila whitei* and the tree-creeper *Climacteris affinis*.

The mulga tracts are continuous, or are made continuous by interdigitation of the dry-country vegetation formations. The small number of plant species composing them and their semi-arid to arid nature necessitate a certain amount of nomadism in their avian inhabitants. Neither isolation nor speciation are to be found in mulga birds.

Barriers: Nil.

(g) Mallee

The mallee extends across southern Australia as a broad, discontinuous belt. The main eastern and western sections, perhaps 700 and 500 miles long, are separated by a gap of some 200 miles. Such differentiation as is occurring in the 10-12 true mallee species (as distinct from those also inhabiting other habitats) occurs between these sections. In *Leipoa ocellata, Drymodes brunneopygia,* and *Pardalotus xanthogpygus* there is no differentiation. It is slight in *Pachycephala inornata, Cinclosoma castanotum, Psophodes nigrogularis, Glossopsitta porphyrocephala,* and marked in *Stipiturus malachurus.* In *Myzantha* the eastern mallee form has now reached species status (*M. melanotis*). In the genus *Pachycephala* there is no doubt that the eastern species *P. rufogularis* also originated and developed in that section. *Amytornis striata* and *Calamanthus* (*fuliginosus*) *campestris,* ranging widely through the arid country of the western half of the continent, have distinctive isolates in the southeastern mallee.

The distribution of mallee is associated with special edaphic, as well as rainfall, factors. The gap at the head of the Great Australian Bight (Nullarbor Plain) is due to edaphic, as well as rainfall, factors. Mallee occurs only on alkaline (limy) sands and is absent from stony lateritic areas.

(h) Desert (Spinifex) Grassland

(i) Stony (Gibber) Desert

Arid sand-desert, with its large clumps of *Triodia* or porcupine grass, provides a limited but specialized habitat for several bird species, especially members of the genera *Amytornis* and *Malurus,* and *Stipiturus ruficeps.* The bare gibber deserts are the homes of *Ashbyia lovensis, Aphelocephala pectoralis,* and *Cinclosoma cinnamomum.* The two groups are differently adapted, dense cover being just as important to the former as it is unimportant to the latter.

The spinifex association is somewhat broken up by salt lakes, gibber desert, and tracts of mulga. Only in *Amytornis*, however, do morphologically differentiated isolates occur.

(j) Mangroves

Whilst mangroves extend discontinuously right around the Australian coastline, only in the northern two-thirds do specialized mangrove bird species occur.

In contrast with the other vegetation formations little precise information is available in the distribution of, and gaps in, the mangrove forests. Much isolation and speciation is taking place in mangrove bird species, however.

Distinctive bird forms occur in the following areas: (i) Shark Bay (*Butorides striatus, Zosterops lutea* (barely distinguishable), *Pachycephala lanioides*); (ii) Midwestern Australia, especially the Ashburton and Point Cloates sections (*Pachycephala pectoralis, P. lanioides, Gerygone* (*magnirostris*) *tenebrosa;* (iii) Derby-Fitzroy River area (*Pachycephala pectoralis*) or Derby-Kimberley area generally (*Zosterops lutea, Butorides striatus, Gerygone laevigaster*); (iv) Northern Territory-Arnhem Land (*Pachycephala simplex, Zosterops lutea, Gerygone laevigaster, Butorides striatus, Pachycephala lanioides, Cracticus quoyi;* (v) Northeastern Queensland (*Pachycephala simplex, Butorides striatus, Cracticus quoyi*); (vi) Eastern and southeastern Queensland. The species *Meliphaga fasciogularis* and *Gerygone cantator* are confined to this last sector.

The mangrove heron, *Butorides striatus*, has the maximum number of morphological forms amongst the mangrove species. The distribution of these forms corresponds generally to those in other mangrove species, as shown in Figure 8.

Known gaps in mangrove distribution include the arid Eighty Mile Beach section and stretches of rocky and sandy coastline along the north (see Vegetation Region map in Atlas of Australian Resources). In addition the mangrove forests themselves vary in nature from place to place, some being sparse and open, others relatively damp and luxurious. They are best developed in inlets and along the lower stretches of rivers.

(k) Swamps, Marshes and Streams

This habitat, covering only an insignificant area of the continent and being best developed in the southeast, has a rich and specialized avifauna. Most water-birds wander widely, however.

A few species have morphologically differentiated isolates in southwestern Australia and/or Tasmania, e.g. *Megalurus gramineus, Porphyrio porphyrio.* The barriers are the arid Nullarbor Plain and Bass Strait.

(l) Miscellaneous Habitats

The pigeons *Lophophaps plumifera* and *Petrophassa albipennis-rufipennis,* requiring rocky outcrops, are broken up into morphologically differentiated isolates by tracts of country lacking in, or having only small areas of, this habitat. Sandplains and sand-hills, the bulk of which would probably stem from the onset of aridity at the end of the Pleistocene, are important in limiting distribution. The northern species of *Amytornis* are confined to three rugged river systems where broken rock and spinifex or undergrowth occur in combination. In these and other species the distributional barriers are tracts of country deficient in permanent cover.

(m) Bird Species ranging through many Vegetation Formations

There are no barriers to distribution in the case of these species.

Water as an Isolating Barrier

(a) Speciation between Australia and New Guinea

As noted in Section IV (2) the width of Torres Strait is some 100 miles, with the longest water crossing perhaps 70 miles. Its maximum depth in the section immediately to the north of Cape York is only 30 feet. The Strait was dry during part of the Tertiary and on two occasions during the Pleistocene.

An assessment of the importance of Torres Strait as a distributional barrier is greatly complicated by the climatic and vegetation differences between the land-masses on either side of it. The north of Australia is relatively dry, is covered by savannah woodland, and is populated by bird species adapted for this kind of life. New Guinea species, by contrast, are largely inhabitants of tropical rain forest and montane forest. There is only a small endemic savannah woodland element.

For the greater part New Guinea has contributed rain forest genera and species, and a few mangrove species, to the Australian avifauna (see Section IX (a)). Australia is mostly supplying savannah woodland species to the restricted areas of that habitat in southern New Guinea.

At the present time Australia and New Guinea have about 191 species of land and fresh water birds in common. These could be allocated, in terms of origin, as follows:

Species of Australian origin,	about 92
Species of New Guinea origin,	about 66
Origin doubtful	about 33

Of these, perhaps 52 of the Australian species (about 58 per cent) have undergone differentiation in New Guinea and some 53 of the New Guinea species (78 per cent) have undergone differentiation in Australia. The smaller percentage figure in the former case is because large water birds (wanderers) and hawks are prominent in the list.

Apart from currently occurring speciation between the two land masses, it is obvious that many bird groups today are represented by equivalent genera and species in the two areas, demonstrating that the interchange has gone on over a considerable period of time. This is particularly marked in the larger families like the honeyeaters and flycatchers but is seen in the smaller groups as well. Thus, for example, the subfamily Grallinae (Grallinidae) has the monotypic genus *Grallina* in Australia and the monotypic *Pomareopsis* in New Guinea, and a parallel situation, in the Timaliinae, is suggested by *Psophodes* and *Androphobus.* Some of the larger Australo-Papuan genera like *Meliphaga* (Meliphagidae), *Pachycephala* and *Gerygone* (Muscicapidae) have a series of equivalent species in the two land masses.

(b) Speciation between Australia and the Near Offshore Islands

Islands are few in number off the Australian coast. Tasmania alone is a large island capable of supporting a moderate-sized differentiating avifauna. Three of the smaller offshore islands have several minor races: King Island in Bass Strait, Kangaroo Island off southeastern South Australia, and Melville Island off Arnhem Land.

The Australian offshore islands on which differentiating forms occur, their distance from the mainland, and the names of the forms are listed in Table 8.

The total number of morphologically differentiated isolates on the offshore islands (including semi-species but excluding cases of speciation by double invasion) is 63. This figure represents about 34 per cent of the total, a somewhat high figure.

Almost all of these, however, are on Tasmania.

(c) Speciation between Australia and the More Remote Islands

The position of the major islands and their distances from the Australian continent are discussed in Section (IV) and are shown in Figure 2. Their avifaunal relationships with Australia are summarized in Table 9.

Apart from New Guinea, it will be seen that a significant two-way faunal interchange has only occurred between Australia and Timor. This island, moreover, lies on a main immigration route from Indonesia to Australia, and vice versa.

Australia has supplied species to New Caledonia, Lord Howe Island, and New Zealand, over a period, but there is no indication of the continent having received new land and freshwater bird species from these sources.

The avifaunal relationships between the more remote islands and Australia may be summarized as follows:

Timor: The breeding land and freshwater avifauna of this island possibly totals 130 species, to which various chance visitors must be added. Oriental and endemic elements are pronounced, though repeated interchange with Australia has occurred. Mayr (1944b) lists 22 bird species that have obviously entered Australia from Timor and points out that Australia has contributed a least 17 species to the avifauna of the island.

New Caledonia: The land and freshwater avifauna totals 68 species, out of which about 18 species are colonizers from Australia. The island has a monotypic family, the Kagu (Rhynochetidae).

Several of the Australian colonists have reached, or passed, that stage of morphological differentiation typical of genetic species. These include a robin (*Eopsaltria flaviventris*), a cuckoo-shrike (*Coracina caledonica*), and an owlet-nightjar (*Aegotheles savesi*). The endemic populations of the bustard-quail (*Turnix varia*), the nightjar (*Eurostopodus mysticalis*), a honeyeater (*Myzomela dibapha*), and others, are racially distinct. There are no apparent instances of "speciation by double invasion."

Lord Howe Island: The avifauna of this island is drawn from New Caledonia and the other islands to the north, New Zealand, and Australia. Several of the European species occurring on the island are self-introduced from New Zealand. The genus *Zosterops* has invaded the island twice though whether or not this has been from a single point source is uncertain.

Of the 20 or more species of land and freshwater birds breeding on Lord Howe Island some 5 are of Australian origin. Of these the fantail *Rhipidura cervina* is now fairly distinct, the eracticid *Strepera graculina* (*crissalis*) and the white-eye *Zosterops lateralis* (*tephropleura*) somewhat less so.

New Zealand: The breeding land and freshwater avifauna amounts to some 80 species, plus over 20 "stragglers" that occasionally arrive from Australia.

Several unique families of birds are confined to New Zealand: the kiwis (Apterygidae), extinct moas (Dinornithidae and Anomalopterigidae), bush wrens (Xenicidae), wattled crows (Callaeidae), as well as aberrant genera like *Nestor* and *Strigops* (parrots).

Australia has had an important influence on the development of the avifauna, with colonization proceeding over a considerable period of time. Some of these colonizers are now generically, others specifically, or racially, distinct. The Meliphagidae are represented by a couple of endemic genera in New Zealand. In the case of the robin-like flycatchers one genus is endemic (*Miro*) and the other (the Australian *Petroica*) has given rise to a species (*P. macrocephala*) in the islands. The stilts *Himantopus novaezealandiae* and *P. leucocephalus* (race *albus*) represent a case of speciation by double invasion. The flycatcher *Rhipidura fuliginosa* has only differentiated to the race level (*fuliginosa*), as has the kingfisher *Halcyon sanctus* (*vagens*). In more recent times an additional 8 to 10 Australian species have colonized New Zealand (see list in Falla (1953)) and now breed there. The latest of these is the swallow *Hirundo neoxena*, which became a breeding species in 1958. These forms have yet to differentiate in the new environment.

(d) Radiation of Australian Species in the Archipelagos of the Southwest Pacific

Many bird species that are obviously of Australian origin, or that can reasonably be inferred to be such, are represented by a series of insular isolates in the southwest Pacific area. These are discussed in Section XIII. They include *Accipiter novae-hollandiae*, *Nycticorax caledonicus*, *Dupetor flavicollis*, and *Petroica multicolor* (Table 9). In some cases the initial range extension would appear to have taken place through New Guinea but in others it has apparently been by way of New Caledonia.

X. HYBRID ZONES AND STEPPED CLINES—EVIDENCES OF FORMER ISOLATION

Hybrid zones and stepped clines occur in many bird species and in various parts of the Australian continent. They are not, however, common (see Table 3). Hybridization in Australia has not yet been subjected to a proper study. This will be necessary before the relative status of *Gymnorhina tibicen* and *G. leuconota, Barnardius zonarius* and *B. barnardi, Sericornis maculatus* and *S. frontalis, Platycercus eximius* and *P. adscitus,* can be determined.

Hybrid Zones

Some of the more common cases of hybridization and the circumstances surrounding them are as follows:

(i) *Northwestern Australia:* Hybridization occurs between the Hamersley and Kimberley races of *Dacelo leachii, Coracina novaehollandiae,* and *Geopelia humeralis* to the north of the Eighty Mile Beach arid barrier, some individuals of the southern forms having managed to bridge it. The Hamersley population of *Ocyphaps lophotes* intergrades both with its counterparts in the Kimberleys and in central Australia, indicating a generalized range extension in this species.

(ii) *Northern Territory:* The northwestern and eastern races of *Poephila bichenovii* hybridize in the general region of Alexandria Downs, N.T. (map in Keast, 1958f), the result of the eastern race having secondarily extended its range westward across the dry country at the head of the Gulf of Carpentaria.

(iii) *Base of Cape York:* Two races of the finch *Poephila cincta* hybridize in this area. One obviously developed on Cape York and the other in eastern Queensland. Contact is the result of both having extended their ranges outwards into the dryer intermediate country.

(iv) *Tip of Cape York:* The small water-kingfisher *Alcyone pusilla* has a variable population here, apparently due to the intrusion of genes from either the northwestern or New Guinea race, or both.

(v) *Darling Downs and northeastern New South Wales:* There is occasional hybridization between the parrots *Platycercus eximius* and *P. adscitus* in this region. It is not clear which of the above has invaded the range of the other but the one obviously developed in the southeast and the other in the northeast of the continent, respectively. (Fig. 12)

Intergradation between the three eastern races of *Malurus lamberti* occurs in this sector.

(vi) *Southern New South Wales and northern Victoria:* In the genus *Gymnorhina,* a white-backed form occupies the southern parts of the continent (*leuconota*), and a black-backed one (*tibicen*) inhabits New South Wales and Queensland. A hybrid zone, corresponding generally to the Murray Valley but in places swinging 50-100 miles to the north, or south, of it connects the two forms today. The zone of hybridization is perhaps 800 miles long. The habitat of *Gymnorhina* is open grassland with scattered trees, a form of association that has vastly increased as a result of clearing of the country.

The possibility that there may be a broad hybrid zone in the striped-crowned pardolates (Dicaeidae) in this section of the continent, with *Pardalotus ornatus* itself being a hybrid form, has already been discussed.

(vii) *Southeastern South Australia: Platycercus elegans* has a series of distinctive intermediate populations in this section connecting the typical form (on Kangaroo Island) with *flaveolus* in the Murray Valley. Cain (1955) suggests that these forms, and *flaveolus* itself, represent former isolates that developed in forested pockets during a more arid phase and that hybridization is the result of secondary range extension.

Further instances of hybridization in South Australia occur as a result of the eastward spread of *Barnardius zonarius* and *Sericornis maculatus,* these meeting their counterparts (*B. barnardi* and *S. frontalis*) in the Flinders Range and Cape Jervis-Mount Lofty sections, respectively. It is not known whether hybrids are rare or common.

(viii) *Complicated Continent-wide Hybridization Patterns: Neositta chrysoptera superspecies:* This case, studied by Mayr (1950b) is illustrated in Figure 21. Mayr has recorded intergradation between the southwestern and southeastern forms in western Victoria and between the southeastern and central Queensland forms in northeastern New South Wales. Thereafter, a series of somewhat transitional forms tend towards the Cape York one. The status of the northwestern counterpart is unknown since it is apparently still isolated from the north-eastern ones. Here too, however, there has been considerable secondary range spread.

Neositta is of particular interest in several ways:

(a) The geographic counterparts had reached a significant degree of morphological difference, with many characters involved, before the barriers broke down or were abridged. (b) Hybridization has simultaneously occurred in many places. (c) In some cases hybrid zones are narrow, in others broad. (d) Many of the areas where hybrid zones and range extensions occur are paralleled in other groups. The two western forms, for example, reflect the generalized eastward expansion that is taking place in various northwestern and southwestern forms (Keast, 1956a).

Pachycephala pectoralis. This species, also analysed by Mayr (1954a), has a peripheral distribution, in the course of which it occupies a wide range of habitats. It has no fewer than 12 geographic races, 8 to 9 of which are apparently isolates. Minor hybrid zones connect the others which occur in the following areas: western Victoria, southern New South Wales, southern Queensland (probably), and Gulf of Carpentaria. Minor hybrid zones such as occur in this species are also to be seen in a few others, e.g. *Zosterops lateralis.*

Hybridization in Australia would appear to result from two main situations: (a) range extensions across or around arid barriers (inferring a minor improvement in the continental climate and probably some secondary adaptation to dry conditions) and, (b) outward movements made possible because of man-made alterations to the vegetation. The majority of cases are attributable to the former but the hybridization between *Gymnorhina tibicen-hypoleuca* in the Murray Valley area has undoubtedly been accelerated, if not caused, by the wholesale clearing of the land and creation of great areas of the "open field" type habitat of this species. Hybridization between *Platycercus eximius* and *P. adscitus* in the Darling Downs and north-eastern section of New South Wales is presumably also partly due to these causes.

(2) Stepped Clines and Lesser Zones of Intergradation

The frequency of occurrence of stepped clines in Australia cannot, at the present state of knowledge, be judged. They too are probably not common, however.

Good examples of stepped clines are provided by the eastern and western forms of the bower-bird *Chlamydera nuchalis* in the region of the Gulf of Carpentaria, and by northern and southern forms of the goshawk *Astur fasciatus.* There is another in *Estrilda temporalis* in the Cairns-Mackay region. Certain of the minor zones of contact, e.g. in *Pachycephala pectoralis*, are possibly more correctly described as stepped clines than hybrid zones.

Various lesser races of birds intergrade in different parts of the continent but the circumstances are too little known to warrant discussion, e.g. in *Cracticus nigrogularis* in the Northern Territory and *Gymnorhina tibicen* along the Queensland-New South Wales border. In the genus *Calamanthus,* however, the intergradation of the forms *campestris* and *fuliginosus* in the Eyre Peninsula and Coorong areas of South Australia is almost certainly secondary.

Not to be confused with the above are instances of colour change along a zone of steep climatic gradient, e.g. in *Smicrornis brevirostris* and *Dacelo leachii.* No isolation has been involved here (Keast, 1957d; 1958h).

XI. THE AUSTRALIAN ENVIRONMENT OF THE PAST AND FORMER SPECIATION. ZOOGEOGRAPHIC SUBREGIONS, THE REFUGE CONCEPT, AND ORNITHOLOGICAL EVIDENCE OF PAST CLIMATIC CHANGES.

Past climatic and physiographic changes on the Australian continent must briefly be reviewed with the objective of determining if: (a) substantially different moulding forces operated during the development and radiation of the major bird groups; (b) the circumstances of origin of specialized avifaunas can be determined; and (c) factors influencing speciation in the past have been substantially different from those operating today.

Characteristics of the Tertiary, Pleistocene, and early Recent in Australia

Tertiary: The restricted information available indicates the following: (i) The continent was flat throughout and there were protracted periods of still-stand. (ii) New Guinea and Tasmania were in continuity with the mainland for part of the time. (iii) Extensive freshwater lakes occurred in the interior. (iv) Vertical earth movements initiated some of the major physiographic features of today: the Eastern Highlands or Great Divide, the Mount Lofty and Flinders ranges in South Australia, and the Spencer and St. Vincent gulfs, the latter deep coastal indentations that were to act as further barriers to west-east distribution. The Olary Ridge arose astride the southward drainage of Lake Eyre into the sea. (v) The climate was humid and warm. (vi) There was a pan-Australian, broad-leafed, mesophytic flora, for much of the period with trees such as *Cinnamomum* and *Nothofagus* prominent. In the late Tertiary, however, xeric elements like *Eucalyptus* and *Acacia* became ascendent.

Pleistocene:

(i) The continent continued to be flat. (ii) The Great Divide was further elevated in early Pleistocene (or late Pliocene), so that new erosive cycles were initiated. The Great Australian Bight was formed by down-faulting. (iii) Sea-level changes occurred in association with the glacial periods in the Northern Hemisphere, major falls of 250-300 feet twice bringing New Guinea and Tasmania into broad contact with the continent. (iv) Glaciation was negligible in continental Australia, never more than a few hundred square miles being affected. (v) Over large areas of the continent, and for a good portion of the Period, the rainfall was reasonably high. Deep alluvial deposits of Pleistocene age are known from many parts of the continent. The central lakes continued to hold water. (vi) Fossil remains show that giant herbivorous marsupials continued to range widely over the continent. Crocodile fossils are known from South Australia, and elsewhere in the south, hundreds of miles beyond their present distribution. One of the southern lungfish fossils is apparently also Pleistocene. (The Pleistocene flora, unfortunately, is virtually unknown.) (vii) The continent was subject to climatic oscillations, although the extent and number of these is not known. Various geologists, and the climatologist Gentilli (1949) have taken the view that the whole continent passed through periods of generalized wetness and dryness at these times. Possibly more generally acceptable, however, in that it accords with the theory of shifting wind belts, is that the arid belt oscillated between south and north (Keble, 1947). That is to say, whilst the south was "wet" the north may have been "dry," and vice versa.

Three to four climatic oscillations, to accord with the number of glacial periods in the Northern Hemisphere, apparently occurred. The geologist Fairbridge (1953) has suggested, however, that the rainfall would have been increased at the height of each Northern Hemisphere interglacial as well as glacial period, with each change being marked by a somewhat dry period. This would mean that the south of the continent may have had as many as eight ''pluvial periods'' of varying intensity during the Pleistocene. Apart from these considerations, however, an increase in the continental area in the north, the result of a fall in sea level, might well have had the direct effect of causing aridity over this section (C. F. Brooks, in Mayr, 1944b).

Soil evidence, believed to support the series of climatic oscillations in the Pleistocene (Butler, 1956) is now believed to refer, in the main, to later climatic fluctuations (Butler, personal comm.).

Early Recent: Widespread aridity followed the end of the Pleistocene. In northern South Australia, central Australia, and parts of Western Australia, the Northern Territory, and Queensland, there was a wholesale drying up of rivers and lakes, by now deeply silted. That the onset of the great aridity, as it has come to be called, was sudden and drastic is shown by the soils becoming freely exposed to wind erosion over a wide area (due to the inability of the plant cover to adapt quickly), and dune systems being built up (Crocker and Wood, 1947). Thus, with the advent of the Recent period the continent came to assume its present form of an arid land mass surrounded by peripheral strips and pockets of fertile country. There is uncertainty as to when the ''maximum aridity'' occurred. Provisional radiocarbon dates, however, indicate that the last of the giant herbivorous marsupials may have died out as recently as 13,000 years ago (Gill, 1955), or even 7,000 years ago (R. Tedford, personal communication).

The evidence today is of some minor climatic improvement. Dune systems are vegetated in places and there has been secondary range spread of various plant and animal species.

Former Radiation and Speciation in Australia

It is obvious that the changes in the Australian continent since the beginning of the Tertiary have been of the most profound kind. From a well-watered, well-vegetated land mass supporting a mesophytic flora, it has changed, through a series of climatic oscillations, to an arid continent on which this flora is confined to a few peripheral sections and pockets.

The original development and radiation of the Australian fauna took place under climatic conditions vastly different from those today. The nature of these earlier isolating barriers are difficult to assess.

The "great aridity" of the early Recent obviously had the most profound implications. Prominent elements like the giant herbivorous marsupials were exterminated. The then-existing flora and much of the fauna of the interior must have been eliminated or else compressed into pockets where conditions were less severe. The relict distribution patterns of animals like *Sarcophilus* (Tasmanian Devil) and *Thylacinus* (Tasmanian Wolf), whose fossils are known from western New South Wales and Western Australia, stem from this period. The lungfish *Neoceratodus* is now confined to the Burnett River, Queensland, and crocodiles to the northern coastal regions of the continent. The dryness of the Australian continent today (one-third arid, one-third semi-arid), the dominance of the dry-adapted animals and plants over the greater part, and the present-day distribution of the various vegetation formations are thus, in effect, relatively recent.

In contrast with its climate, the Australian continent has not altered physiographically to any great extent. Nevertheless, the elevation of the Great Divide in eastern Australia in the late Miocene, and its further development in the early Pleistocene has been of great significance. The Great Divide influences precipitation over a large section of the east (giving it a uniform rainfall instead of one largely confined to the winter or summer). Its presence ensures a considerable habitat diversity in the continent. All the rain forests, and most of the sclerophyll forests, are confined to it. The Great Divide is the major "refuge area" in which "fertile-country" animal species (and a good proportion of the unique endemics come in here) are able to persist. Again, many of the tropical New Guinea elements that have colonized the northeast have been able to do so because of the conditions created by the northern end of the range. The abrupt changes in climate and vegetation along the top and western slopes of the Great Divide are the limiting barrier to many species.

A second physiographic development consists of the mid- and late-Tertiary changes in South Australia: (i) the formation of the St. Vincents and Spencers Gulfs, and the Great Australian Bight, by down-faulting and, (ii) the elevation of the Mount Lofty and Flinders Ranges and of the Olary Ridge. The Bight along with climatic and edaphic factors, was to take over from the intrusive Cretaceous sea the maintenance of major floristic differences between east and west. The Mount Lofty Ranges today support a pocket of sclerophyll forest in what would otherwise be dry country. The elevation of the Olary Ridge, across the drainage of Lake Eyre into the sea, and the damming back of the steadily silting lake, must have had a local influence on animal distribution subsequently.

Little can be said of the circumstances of origin of the ''specialized avifaunas'' of today except that it is doubtful if any are particularly recent. It has been suggested by the writer, in contrast to the views of certain geologists who have postulated periods of fairly uniform fertility during the Pleistocene, that some desert must have been present on the continent throughout. This is because Australia has a number of unique and highly specialized desert elements, e.g. the marsupial mole (*Notoryctes*), the devil lizard (*Moloch*), and the tree *Casuarina decaisneana*. These have obviously had a long history (Keast, 1959a). The genus *Amytornis* is the nearest approach to a true desert genus amongst the birds, though there are quite a number of desert species within genera.

Much of the sclerophyll avifauna is obviously old, as are many of the savannah woodland elements. On the other hand, mangrove species and, with one or two exceptions, rain forest species, are fairly recent immigrants from the tropics.

Wood (1959) has stressed that the major Australian plant communities, though stable, are relatively young. There has undoubtedly been a long standing tendency, however, for rainfall and vegetation formations to have a zonal distribution, and for the components to bear a relative relationship to each other.

It is obvious that speciation patterns prior to the onset of aridity would not have been the same as those operative today. Nevertheless, the fact that ''refuge areas'' are centred on hilly or mountainous segments that have been relatively constant in position since the Tertiary (though not elevated nor eroded to the same extent) suggests that they may have, over a period, been centres of origin of new forms. As noted, the differentiation of New Guinea immigrants in Australia has been occurring continuously.

The key to much of the Pleistocene and Recent speciation undoubtedly lies in the climatic oscillations to which the continent has been subject. A much better understanding of these is needed. This particularly applies to the history of the Nullarbor arid barrier, isolating the very interesting faunas of southeastern and southwestern Australia. In this regard it has been reasoned that every south-north shift in the continent's centre of aridity would lead to a tongue of better watered and better vegetated country extending across the head of the Great Australian Bight. Speciation in some birds (*Psophodes*, *Eopsaltria*, *Pachycephala inornata-rufogularis*), various frogs (Main, Lee and Littlejohn, 1958), and tabanid flies (Dr. I. Mackerras, personal communication) would appear to be explicable only in this way — waves of east-west colonization by animal species, occurring with each improvement.

Several of the major distributional barriers of today would have been eliminated or made less effective, not only by changes in rainfall, but by changes in sea level. A relatively small fall in sea level would have rendered the Gulf of Carpentaria dry land and permitted a much greater flow of forms between the northwest and northeast. The reduction or elimination of Bass and Torres Straits must also have led to a greatly accelerated interchange of forms with Tasmania and New Guinea.

Each climatic shift in Australia has undoubtedly modified and altered the vegetation pattern. With each major change some bird species must have prospered and expanded their distribution, others become more restricted, and others undergone new adaptations. New forms and species that had developed at some isolated ''point source'' could have undergone marked increase in range at these times. Those that had reached species status could have come, or been forced, to occupy new habitats adjacent to those of their parents. In other cases, hybrid belts would have been formed. Lastly, amongst the various adaptations would be some with indirect evolutionary consequences, e.g. from a sedentary to a nomadic way of life, and vice versa.

The Zoogeographic Subregion Concept in Australia

The concept as it applies in Australia has recently been discussed by the writer (Keast, 1959c), and the various subdivisions as advanced by workers in the different zoological groups have been reviewed. The conclusion was reached that, so far as the concept has a place in Australian zoology, the scheme of Baldwin Spencer (1898), with its three simple subdivisions (see later), is the most natural arrangement. The Spencer scheme has recently been modified and adopted for birds by Serventy and Whittell (1951). In contrast with the Spencer scheme, the multiplicity of subdivisions advanced by some invertebrate workers were found, for the most part, to correspond to refuge areas, and areas of minor isolation, in the higher vertebrates.

The scheme of Spencer, derived originally from a study of mammals, frogs,[1] etc., is as follows:

Bassian Subregion: Forested coastal regions of New South Wales and southeastern Australia, including Tasmania. The isolated southwest corner is also rich in Bassian elements. The Bassian region corresponds closely to the limits of the sclerophyll forests in Australia.

Torresian Subregion: Forested coastal regions of the north and northeast of the continent. This element is mostly of New Guinea origin. The zone corresponds approximately to the limits of tropical rain forest and tropical savannah woodland, though elements penetrate south for varying distances down the east and west coasts.

Eyrean Subregion: Dryer interior of the continent, and extending to the coast in the south and west, especially where the arid country extends to the sea.

To what extent these divisions can justifiably be regarded as ''areas of origin,'' as distinct from ''faunistic blocks'' linked by common needs in the way of climate and vegetation and adaptations to environment, it is difficult to say. The Bassian zone, as noted, is a refuge area where various old ''wet country'' species and forms have been able to persist. The Torresian sector retains its distinctness to a degree because it is the sector of the continent in which new arrivals from the north establish themselves. In places, the division between the regions is fairly sharp, so far as birds are concerned. This applies as between the Bassian and Eyrean species in inland New South Wales. On the other hand, the postulated line separating Bassian and Torresian elements in the coastal sector has little foundation. Individual Bassian, Eyrean, and Torresian species more often than not do not extend to the limits of their individual region but occupy only part of it. Again, and as would

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[1] In a recent comprehensive study of the Australian amphibian fauna, Dr. J. R. Moore (personal communication) has concluded that frog distribution patterns do not justify the recognition of zoogeographical subregions in Australia.

be expected, there is a varying degree of penetration by individual species from one region to another. This factor has caused Serventy and Whittell (1951) to reiterate that the zoogeographic subregion concept is only valid if used in the "fluid," rather than the static, concept.

It is doubtful if anything is to be gained, from the speciation viewpoint, in trying to analyse the Australian avifauna from the zoogeographic subregion, rather than from the vegetation formation, viewpoint. The vegetation formation is a much more real factor in bird distribution. Each of the basic vegetation formations has a series of bird species, and sometimes even groups, confined to them. These, along with an associated quota of plant and other animal species, live under common biotic and physical conditions and can readily be referred to by the terms "sclerophyll forest fauna," "savannah woodland fauna," and so on.

The Refuge Concept in Australia

Bird workers who have discussed aspects of the refuge concept in Australia include Gentilli (1949), Mayr (1950b), Serventy (1951), Condon (1954), Cain (1955), and Keast (1957e). As yet, however, no attempt has been made at a comprehensive survey or study of the major refuge areas on the continent and their characteristics. It is basic that, if the refuge theory has a real application in birds, there must be a large measure of consistency, from group to group, in the areas that have acted as "refuges."

"Relict type" distributions have long been recognised by Australian biologists: see the botanists Crocker and Wood (1947) and the entomolgist Tindale (1949) with respect to the plants and butterflies, respectively, of South Australia. It must, however, be recognised that birds, with their moderate capacity for dispersal yet reluctance to cross hostile areas, and moderate to large body size (requiring a reasonably large area to survive), are more likely to reveal what are the basic refuge areas in Australia than plants or invertebrates with little capacity for dispersal.

Figure 27 shows the major refuge areas in Australian birds as indicated by the present survey. The black arrows, and letters, indicate the barriers that isolate them.

These refuge areas have the following characteristics:

(a) Each is an area of hilly or mountainous terrain (see Fig.

3), has a higher rainfall than the surrounding country, and hence provides a measure of protection from seasonal and long-term shifts in climate. It has a distinctly richer and more diverse vegetation than its environs.

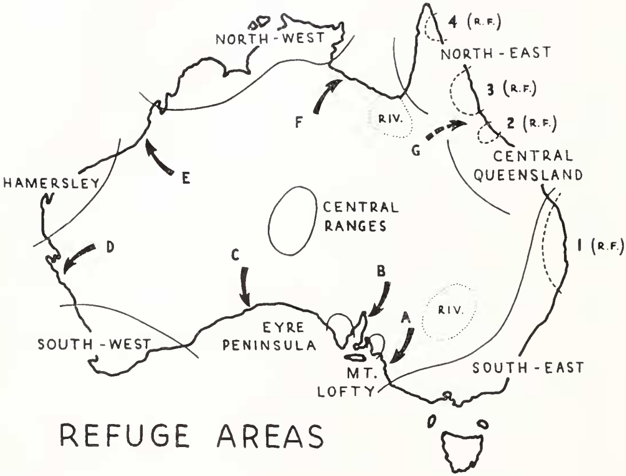

Fig. 27. Refuge areas (which are also major centres of isolation) on the Australian continent. These are typically mountainous or hilly sections, as follows: southeastern section of Great Divide, Mount Lofty Ranges, Eyre Peninsula, southwest corner, Hamersley section, northwestern section, northeast (Cape York), central Queensland, and central ranges. These are of the greatest significance in sclerophyll forest and savannah woodland species. Mangrove species are, however, isolated in the Hamersley, northwestern and northeastern segments, and a few rain forest — monsoon forest species as between the northeast and northwest.

The numbers (1-4) indicate the major rain forest refuges.

In the case of a few bird species (especially parrots) river systems have acted as refuges. The Murray-Darling basin has been of importance in a few species and the rivers entering the Gulf of Carpentaria in one.

The black arrows and capital letters indicate the major isolation barriers (see text).

In the case of a few of the parrots and one or two other bird species, river systems act as refuge areas. Riverine refuges have been earlier recognised for certain plants by the botanists Crocker and Wood (1947).

(b) Most contain more than one basic vegetation formation.

(c) Each supports several and sometimes a great number of isolated bird populations, forms, or species which in turn belong to a variety of different groups. The most distinctive forms occur between the northeast and northwest, and southwest, of the continent, respectively.

These major refuge areas, summarized in Figure 27, are as follows:

(a) *Northwest corner (especially Arnhem Land):* Many savannah woodland, monsoon forest and, to a lesser degree, savannah grassland and mangrove forms are isolated here. A number of them have reached a significant degree of differentiation. For examples see Figures 12, 21, 22 (savannah species), and 8 (mangrove species). This is also a somewhat important area in the case of plants and various other animal groups.

(b) *Northeast corner (especially Cape York):* Savannah woodland, rain forest, and a few mangrove species have isolates here. Since, however, most rain forest and mangrove forms have secondarily been derived from New Guinea, the hilly sections of Cape York have only really functioned as a refuge in the case of some savannah species. Many of the latter are counterparts of those in the northwest. For examples see Figures 12, 21, 22.

(c) *Central Queensland:* Unlike the others this is not a compact area but is somewhat vague and ill defined. That it is really a series of minor refuge areas is indicated by the multiple geographic forms in *Platycercus adscitus* and *Neositta* (Figs. 12 and 21). Again, several restricted areas of higher elevation rise above the Great Divide which is rather low here, giving rise to rain forest pockets. These areas are Atherton, the Clarke Range (adjacent to Bowen and Mackay), and Bunya Mountains.

In addition to the above, there is a degree of isolation and differentiation between various savannah woodland inhabitants of central Queensland and those of Cape York, e.g. *Seisura inquieta* (Fig. 15), *Climacteris picumnus* (Fig. 22), and *Poephila cincta*.

Central and southcentral Queensland are populated by a series of distinctive elements in the case of land snails (McMichael and Iredale, 1959), whilst several distinct species of reptiles are confined to this sector (Keast, 1959c).

(d) *Southeast of continent:* This extensive mountainous strip extends from the Bunya Mountains in southern Queensland to central-western Victoria. It is rich in endemic genera and species in all animal groups and is by far the most important of the refuge areas. Sclerophyll (mostly), rain forest, and savannah woodland elements are contained within it. At the same time, some subsections within it are of importance on their own, e.g. Macpherson-Dorrigo rain forests, Koskiusko Plateau (in invertebrates). Insular Tasmania, with its many indigenous species and races is an isolated segment. Examples include those shown in Figure 12, 21, 22.

(e) *Mount Lofty Ranges and Kangaroo Island:* These sclerophyll sections are minor refuges, and various populations isolated there have reached a minor degree of differentiation. One such is indicated in Figure 19.

(f) *Eyre Peninsula:* This functions as a minor refuge area for a couple of savannah species of southwestern origin (e.g. *Climacteris rufa occidentalis*, Fig. 22).

It fulfills a similar role in the case of various plants (Wood, 1959) and some invertebrates.

(g) *Southwestern corner:* This is an important refuge area. It contains one monotypic bird genus and a couple of dozen forms that have differentiated to varying degrees from their counterparts in the sclerophyll forests of southeastern Australia. Many others are isolated but undifferentiated. Nevertheless, its importance in birds compares in no way with that in plants, 75 per cent of the species of which are endemic to the region. About 8 monotypic reptile and 3 monotypic marsupial genera are restricted to southwestern Australia. For examples see Figures 12, 22, and 23.

(h) *Hamersley area:* Several savannah woodland and grassland bird species have morphologically differentiated isolates here, e.g. *Climacteris melanura* (Fig. 22). The mangrove forests of this section also support various morphologically differentiated isolates (see Fig. 8).

The biological significance of this area is that it contains a somewhat impoverished outlyer of the Kimberley flora and fauna, largely isolated today, mixed with a range of intruding desert elements.

(i) *Macdonnell ranges and other mountain ranges of Central Australia:* A number of savannah species have populations here that are isolated to a varying extent. Only in a couple of cases, however, has differentiation occurred and in each case it is relatively minor; example, *Rhipidura fuliginosa albicauda,* Figure 14. A number of plant species have outlyers here isolated by hundreds of miles from their counterparts in the southeast (see Keast, 1959d).

(j) *The Rain Forest refuges:* These are numbered "1-4" in Figure 27. The Cairns-Atherton tract is by far the most important and it has a large and diverse avifauna. On the other hand, the Clarke Range is apparently only of limited importance. As noted earlier, isolation and differentiation in rain forest species are mostly taking place between the Cape York, Cairns-Atherton, and Bunya Mountains-Dorrigo tracts. The isolating barriers are areas of dry open savannah.

(k) *Riverine refuges:* Where tracts of forest are developed along river systems there is a marked tendency for a richer avifauna than in the dryer surrounding country. Several of the river systems have well differentiated isolates, especially in parrots. These include those draining the Hamersley plateau, the northwest and southwest of the continent and the central ranges. In addition, the Murray-Darling system (see map) has several distinct bird forms including the parrots *Polytelis swainsoni* and *Platycercus flaveolus,* and the rivers draining the Gulf of Carpentaria have one distinct form, the parrot *Barnardius barnardi macgillivrayi.*

Barriers between Refuge Areas

The barriers isolating the refuge areas are, typically, sections or tongues of dry or arid country, as will be seen from the rainfall, climatic and vegetation maps. They are marked "A" to "G" in Figure 27. These have already been discussed in Section IX with respect to breaking up the basic vegetation formations. They may be briefly listed as follows:

(A) Coorong arid section (90 Mile Desert), a tongue of arid country extending south from the interior.

(B) Spencer Gulf, a deep coastal indentation with arid country about its head.

(C) Nullarbor Plain (arid) and Great Australian Bight.

(D) Tongue of arid country extending from the interior to the coast in the region of Shark Bay.

(E) Eighty Mile Beach arid section, a tongue of the Great Sandy Desert extending through to the sea.

(F) Tongue of dry country extending from inland to the head of the Gulf of Carpentaria.

(G) Tongue of somewhat dry savannah country extending to the sea in the vicinity of Townsville. It is easy to see how this belt, perhaps 100 miles wide, should break up the distribution of rain forest species. The fact that a few savannah woodland bird species have differentiated populations to the north and south of it suggests that it may formerly have been more severe.

The Macdonnells and other ranges in central Australia are surrounded by a series of arid tracts, the Arunta Desert to the east, Great Sandy Desert to the west, extensive gibber plains to the south, and stunted desert scrub to the north. These serve today to isolate the animal inhabitants of the central ranges from their counterparts elsewhere in the continent.

As has previously been noted, the rain forest tracts ("1" to "4" in Fig. 27) are isolated from each other by tracts of dry savannah woodland, whilst the riverine refuges are surrounded by flat, more open country.

Some Fragmental Avian Evidence supporting the Postulated Quartenary Climatic Successions

During the present survey, and elsewhere, a limited amount of avian and other evidence that appears to support the postulated south-north movements of the climatic belts has been noted. It is as follows:

Evidence that the north of the continent has been wetter than at present: (a) The distribution of the chat, *Epthianura crocea,* a species requiring somewhat damp river valleys, is now broken up into four populations, respectively 800-900 miles apart (Fig. 16). In former times this type habitat must have been much more common across the north of the continent.

(b) Many of the endemic savannah species in the north have isolated counterparts in the northwest and northeast corners of the continent, respectively (see earlier).

Evidence that the north of the continent has been dryer than at present: The isolated "species" of *Amytornis* along the northern seaboard are examples (Fig. 18a). They are derivatives of the desert spinifex species *A. striatus* and their requirements in the way of cover are such that they could only have reached their present position by a continuous tract of spinifex formerly extending through to the sea in this section.

Evidence that the south of the continent has formerly been more fertile: (a) There are a great many sclerophyll bird species with isolated counterparts in the southeast and southwest of the continent, respectively.

(b) Certain relict bird populations in the mountains of central Australia, i.e. *Rhipidura fuliginosa albicauda*, *Strepera versicolor centralia.*

(c) Certain "relict-type" distributions in southwestern Australia, e.g. *Atrichornis clamosus, Dasyornis broadbenti;* also the persistence of *Phaps elegans* and other species on the Abrolhos Islands, despite their occurring on the mainland only a considerable distance to the south. (Serventy and Whittell, 1951).

Evidence that the south has been dryer: Biological evidence for this is, of course, difficult to find as far as present-day distributions are concerned, for it is scarcely possible for "outlyers" of formerly widespread arid country species to survive in what are now humid zones. A possible example may, however, be the occurrence of a breeding population of the dry country robin, *Petroica goodenovii,* on Rottnest Island, the neighbouring mainland being occupied by *P. multicolor* (D. L. Serventy, personal communication). Again, the secondary range extension outwards from the southwest corner of species like *Neositta* (*chrysoptera*) *pileata* and *Acanthiza pusilla albiventris* must infer a slightly improved climate.

Certain mammalian fossil occurrences are significant. L. Glauert (personal communication) has recorded remains of the dry country bandicoot, *Macrotis lagotis,* in post-Pleistocene cave deposits at the Mammoth Cave, southwestern Australia, where the animal no longer occurs. Similarly, Lundelius (1957) found fossil *Dasycercus,* an arid country dasyurid, as well as *Sminthopsis hirtipes,* in caves north of Perth, many hundreds of miles south of their present desert habitat.

In contrast with the above, Tindale (1949) and Condon (1954) take the view that the persistence of a few relict bird and butterfly populations in South Australia indicate that the climate in this section could not have been materially dryer in the recent past.

Evidence that the south of the continent has been subject to more than one "climatic swing." Evidence for this comes from frogs (Main, Lee and Littlejohn, 1958), tabanid flies (Dr. I. Mackerras, personal communication), birds like *Psophodes olivaceus-nigrogularis* (map in Keast, 1958g) and *Pachycephala rufogularis-inornata* (see Fig. 13), and *Eopsaltria georgiana-australis.*

More examples of double invasion of the southwest by sclerophyll forest bird species might be expected than actually occur. *Eopsaltria georgiana* and *E. australis griseogularis* is, however, a good case of this. The red-backed wrens of the *Malurus lamberti* complex (*M. elegans* and *M. pulcherrimus*) might well be a second, and the zonal races of the thornbill *Acanthiza pusilla* in the southwest, a third.

The way in which various bird genera are represented by distinct species in adjacent and "parallel" vegetation zones could, in point of fact, be evidence of climatic "swings." These species could only have arisen in isolation (possibly during arid phases) and presumably become preadapted to the second habitat prior to the changing climate permitting them to spread out through it as it expanded. It will be noted that Paramanov (1959) has postulated shifts in the temperature zones in association with glaciation to account for the altitudinal zonation of certain fly species in the Australian Alps.

Soil-Vegetation Relationships and the Climatic Past

Soil, next to climate (present and past) and topography, is the chief factor governing the distribution of vegetation. Accordingly, it can be said that the edaphic history of an area and the distribution of the major soil areas today have a basic influence on present day animal distribution. Alternatively, the major soil changes during the Tertiary and Quaternary must have also had a direct bearing on past animal distribution.

As has been noted, the zonal soil groups in Australia follow a similar pattern to rainfall, as will be seen from a comparison of Figures 5 and 6. That they follow a broad but not absolute correlation with much of the zonal vegetation sequence has been stressed by Wood (1959) and others. The maps indicate that this correlation is best between sclerophyll forest and the podsols, mallee and the mallee soils, desert loams and mulga, and desert sandhills and desert grassland.

Soils are highly complex and variable substances and their development and evolution are conditioned by many factors, including parent material, age of land surface, relief, climate (rainfall and temperature), vegetation, and even the fauna.

Again, most soils are polygenetic, the result of more than one combination of soil-forming factors (Crocker, 1959b). The physiographic and climatic changes outlined for Australia have thus, obviously, had a direct influence on soils: mountain building, sedimentation, erosion, wind, vulcanism, fluviatile and arid periods, climatic and rainfall shifts, and plant growth itself. Hence, it must be stressed that a simple rainfall change does not permit the biologist to assume that this would automatically lead to the development, over that section of the continent, of the vegetation association that exists in the equivalent rainfall zone today. The influence of the change may, in point of fact, be direct, or it may be indirect and dependent upon a vegetation or microbiotic succession first creating the necessary soil nutrients.

Unfortunately, little more has as yet been learnt of past soil changes in Australia than of past vegetation changes. Edaphic factors serve to explain the most puzzling, and certainly the most important barrier to plant and animal distribution in Australia today, that serving to isolate the forests of southwestern Australia from those of South Australia and the east. This isolation, originally associated with the Cretaceous and, to a degree, Tertiary seas, has been shown by Crocker and Wood (1947) to have been successfully retained long after the disappearance of the physical barrier by (a) the southwestern forests being specialized for life on lateritic soil, (b) the accession of calcareous loess during the late Pleistocene, resulting in a large area of pedocalcyc soils lying right across their potential routes of colonization to the east plus, of course, the climatic factors already discussed.

XII. "ECOLOGICAL" SPECIATION. THE DEVELOPMENT OF HABITAT DIFFERENCES BETWEEN SPECIES

It has been stressed that the habitat occupied is a "species character" in the case of most Australian birds. Hence, it is important to endeavour to explain the origin and development of these ecological differences.

Two approaches could give this basic information: (1) A survey of the species to show if any vary geographically in habitat occupied (in the way that they vary geographically in morphological characters) and, (2) A study of the ecology of related species occupying adjacent habitats. This should reveal just how great the differences between them actually are and how they might have arisen.

The latter approach obviously requires detailed field studies and hence can only be lightly discussed here. It is, however, a profitable field for future investigation.

Geographic Variation in the Habitat occupied by Species

(a) Habitat Versatility in Species with Broad or Generalised Ranges

Whilst some species are restricted to one vegetation formation, others extend through many, sometimes ranging widely over the continental land mass. In these cases it is to be expected, since the physical and biotic conditions will vary, that extreme populations will differ in their adaptations. Isolation is lacking in species with wide and extensive "interior type" distribution patterns and is unlikely to arise.

However, as suggested by various authors, the severance of any continuously ranging species into two parts would consolidate and increase the ecological differences between the extremes.

(b) Habitat Variation in Species with Peripheral or Specialized Ranges

As noted, it is in these species that the majority of morphologically differentiated isolates occur. Here too many significant cases of geographic variation in habitat accompanying speciation are to be found. A selection of these is as follows:

(i) Within Species

Rhipidura fuliginosa and *Pachycephala pectoralis:* These two species extend, with various isolates, almost completely around the periphery of the Australian continent. Sclerophyll forest is occupied in eastern and southwestern Australia, rain forest in the northeast, monsoon forest in the northwest, and mangroves in the west. *Pachycephala* also occurs, in places, in mallee and *Rhipidura* has an isolated outlyer in the Macdonnell ranges. This habitat variation in *Rhipidura fuliginosa* will be seen in Figure 14.

The common denominator of these habitats is dense cover. Otherwise they have relatively little in common.

Eopsaltria australis and *Climacteris rufa:* Both of these species have a fairly wide habitat tolerance in southwestern Australia, though their headquarters are the sclerophyll forests.

Each has an isolated outlyer in the savannah woodland on Eyre Peninsula to the east of the Nullarbor Plain.

Climacteris leucophaea. This species occupies sclerophyll forest in eastern and southeastern Australia, rain forest in the Cairns-Atherton sector, and mountain forest in New Guinea (see map in Keast, 1957e). The north Queensland and New Guinea races are isolated. The rain forest form (*minor*) is approaching that stage of differentiation typical of a full species.

Strepera vericolor. This is a mountain species in the south east, but it has a derivative in the dry mallee of western Victoria.

Stipiturus malachurus. This species, basically an inhabitant of submarshy heathlands along the coastal fringe, provides an interesting demonstration, in the western part of its range (Fig. 19), of the adaptational pathway to life in the semi-arid mallee and arid spinifex desert.

A derivative, *S. ruficeps*, is isolated in the spinifex desert of the centre of the continent.

(ii) Within Superspecies

Sericornis frontalis — S. humilis — S. maculatus: The habitat in this group extends from rain forest and sclerophyll forest in eastern Australia to dry sclerophyll, savannah woodland, and coastal thickets in the south and southwest of the continent.

Calamanthus fuliginosus — C. campestris: The former inhabits the damp peripheral coastal section, the latter the semi-arid and arid inland. There is a morphological and habitat transition zone in South Australia.

Psophodes olivaceus — P. nigrogularis: The former occupies the wet rain and coastal sclerophyll forests in the east. The latter occupies the coastal thickets and adjacent sclerophyll in the southwest, and the semi-arid mallee of that section and of inland Victoria. That is to say it demonstrates the transition from life in wet to life in dry country (Keast, 1958g).

Amytornis striatus: Here the parental form has an extensive range through the spinifex sandplains of the interior. From it isolated species that live in rock river gorges have been "budded off" around the periphery of the range (Fig. 18a).

Malurus cyaneus — M. melanotus — M. splendens group: In this case a chain of 4 distinctive forms (3 of which are certainly so distinctive that they must be regarded as species) are *isolated* in a series of climatically quite dissimilar habitats from east to west across the continent (Fig. 8). These are: *M. cyaneus* (eastern sclerophyll forests); *M. melanotus* (inland mallee and mulga), *M. callainus* (central spinifex desert), and *M. splendens* (western sclerophyll forest and dry scrub).

Climacteris erythrops — C. affinis: These species are isolated in mountain sclerophyll in the east and arid mulga in the interior, respectively.

Drymodes brunneopygia — D. superciliosus: The former is isolated in the dry mallee association of the interior of southern Australia, the latter in the rain forests of Cape York and New Guinea.

The above instances show not only that the different races of a species (isolated or otherwise) may occupy distinct vegetation formations in different parts of the range but how these habitat differences may develop. Geographically representative species within superspecies sometimes occupy vegetation formations that are almost the opposite extremes of each other.

These cases indicate the probable mechanism whereby adjacent vegetation formations or zones come to be occupied by different members of a genus. It is characteristic of most species to extend outwards to the limits of the occupiable habitat. Where there is geographic variation in habitat the process is, in Australia, not one of the species varying its "preference" from one part of the range to another but of occupying the only vegetation formation available. As with purely morphological characters, isolation tends to consolidate and increase the differences. Thus, for example, amongst sclerophyll forest species *Climacteris rufa* has an isolate in savannah woodland whilst *C. leucophaea* has one in rain forest.

Once an isolate develops habitat differences from its parent, further changes can, presumably, take place in two ways. The habitat to which it is confined could undergo further change or modification, necessitating further adaptive changes on the part of the bird, if it is to survive. Eventually a situation could develop, as in the *Malurus cyaneus* superspecies or *Climacteris erythrops*, in which the different species, isolated from each other, occupy very different habitats. Alternatively, climatic changes could secondarily bring the vegetation formations into a closer position relative to each other so that the forms occurring in them approach or meet along the periphery.

If reproductive isolation has been established in the meantime, one consequence could be that each would remain within, or at least have a preference for, the formation to which it had become adapted. The honeyeaters *Meliphaga melanops* and *M. cassidix* in southern Victoria apparently avoid competition by this mechanism, and it will probably prove to be equally the case with the coastal and interior races of the thornbill *Acanthiza pusilla* in New South Wales.

Competition may, in actual fact, be the final force consolidating habitat differences between related species (see next section).

It goes without saying, in all these cases, that before a species can adapt or develop into a new association that habitat must contain certain characteristics basic to that species. Thus, members of the genus *Malurus* require, at all times, thickets or undergrowth and those of *Climacteris* tree trunks on which to feed. Nevertheless, at a certain stage, feeding and other modifications may manifest themselves, e.g. members of the *Climacteris picumnus* group occupying open country obtain part of their food from the ground.

Some geographic variation in habitat and ecology is undoubtedly characteristic of all widely-ranging species. Those members of sclerophyll species living in southwestern Australia, for example, are subject to somewhat dryer conditions than their counterparts in the east. Alternatively, within any one area, the vegetation is subject to change from time to time, as part of a succession or due to a changing climate.

All in all, it can be said that there is ample indication in Australia of how isolates may diverge and "speciate" ecologically, just as they do morphologically. Some ecological differentiation probably precedes geographic isolation in most instances but there is no need for it to do so.

(c) The Occupation of Adjacent or Nearby Habitats by Different Infraspecific Forms

Instances of this are apparently not uncommon in various montane regions of the world where sharp altitudinal changes in vegetation, and the interdigitation of vegetation zones bring markedly different bird habitats into close proximity. The mountain chains of California provide one such example — see the various publications of Miller and others (e.g. Miller, 1951). These are the kinds of situations that are sometimes considered to be possible instances of sympatric speciation. Ornithologists generally, however, are adamant that sympatric speciation does not occur in birds.

Australia, with its general flatness and arrangement of vegetation formations into broad zones, provides little evidence of this type of race distribution, for barriers are generally broad, not narrow. Speciation is thus clearly seen to be geographic. The nearest approach to the other situations, however, are to be seen in the following cases:

(i) Colour races associated with steep climatic gradients (examples of Gloger's Rule). Examples: *Smicrornis brevirostris* and *Dacelo leachii*. These are purely local clinal forms, however, without a potential for developing into new species.

(ii) Zonal races, in which isolation is present. There are a couple of instances of these in New South Wales. *Acanthiza pusilla* and *Malurus lamberti* each have a coastal race (in sclerophyll) and an interior one (in savannah, etc.). Both are now isolated from their counterparts (though in *Malurus* there is a hybrid zone in northern New South Wales). The interior race of *Acanthiza pusilla* is certainly a secondary invader of eastern Australia for its affinities lie with the southwestern stocks (Mayr and Serventy, 1938).

Another such case is provided by the Samphire Thornbill (*Acanthiza iredalei*) in South Australia (Condon, 1954). Here, three races are isolated in adjacent but different habitats; i.e. it is the same kind of situation as in the species of the *Malurus cyaneus* group (Fig. 8).

Less understood than the above are the colour races (three) of *Acanthiza pusilla* in southwestern Australia (Mayr and Serventy, 1938; Serventy, 1953). As their distributions correspond to general zones of decreasing rainfall their characteristics could be attributed to the Gloger Effect were their ranges not paralleled, to a degree, by three species in the *Malurus lamberti* group of wrens. In the later publication, Serventy (1953) has suggested that the coastal race, *Acanthiza pusilla leeuwinensis*, may actually be derived from the coastal one in the east, by migration around the Bight, and that it has achieved its present resemblance to the inland one by secondary gene flow between them.

Ecological Differences between the Different Members of a Genus Inhabiting the same or Adjacent Habitats

(a) The General Problem: the Situation in "Old" and Well Consolidated Species

The Australian avifauna contains many instances of species within genera specialized for life in different vegetation formations, vide *Meliphaga, Malurus, Gerygone, Climacteris* (Figs. 7, 8).

Some of the larger genera, moreover, have more than one species within a single vegetation formation, e.g. *Meliphaga* and *Acanthiza* in the sclerophyll forests near Sydney. In such cases distinct subzones are occupied. Here, different species of *Meliphaga* inhabit, respectively, the stunted heathlands of the hilltops, areas of saplings and undergrowth, the more open sections of the forest, and pockets of rain forest. Of the five species of *Acanthiza* occurring in the area, two are ground feeders (in different classes of country). One is mainly a low bush and shrubbery feeder. The other two are foliage feeders, with a tendency for the one to inhabit mainly somewhat lush forests in hilly sections and the other dryer sections in more open country. These observations reflect findings from other parts of the world that related bird species occupy slightly different habitats or niches and that direct food competition between them is rare, e.g. Europe (Lack, 1944), East Africa (Moreau, 1948), and California (Miller, 1951). As yet no comparative work on the finer ecological attributes of related bird species has been carried out in Australia. It could be, however, in view of their generalized similarity in bill form, that in most cases no more profound food differences separate the occupants of adjacent habitats than those directly associated with the habitats themselves. Most bird species are now recognised as being somewhat opportunistic feeders (Lack, 1954; Hinde, 1959, and others). Where, however, closely related species co-exist in a single habitat they tend to be specialized for different foods (Lack, 1954).

(b) Recently evolved Species. Habitat Differences in cases of Marginal Overlap and Double Invasion

In all cases of marginal overlap of recently evolved species in Australia there is at least some tendency for different habitats to be occupied. This indicates not only that slightly different "preferences" have been built up during the isolation but emphasizes the role of competition in consolidating, if not initiating, ecological differences.

The habitat relationships in the overlap area in the cases of recently evolved species are as follows:

(i) *Amytornis textilis* and *A. modestus* (Fig. 17a) in the Macdonnell Ranges. The former lives in spinifex on the hills and the latter (which is apparently the invader) keeps to spinifex in the valleys. Elsewhere, similar or equivalent habitats are occupied.

(ii) *Philemon argenticeps* and *P. novaeguineae* (Fig. 26) in northern Australia. In this instance the former, the older resident in Australia, occupies the savannah woodland and grassland belts extending, in places, well out into the dryer forests. The later invader keeps to the peripheral mangroves and damper savannah woodlands of the coastal strip.

(iii) *Meliphaga virescens* and *M. versicolor* (Fig. 25). In this case the parental species (the former) occupies the dryer interior and its derivative (which arose in New Guinea) has re-entered Australia to occupy the mangrove habitat.

(iv) *Melithreptus lunatus* and *M. albogularis* (Fig. 23). In eastern Queensland, where these species overlap, the former (the southern species) keeps to the highlands and the latter (the invader) to the lower country.

(v) *Meliphaga lewini* and *M. notata* (Fig. 24). These two species have the same sort of relationship in the Atherton area, where they overlap. The southern *M. lewini* is only to be found in the highlands.

(vi) *Pachycephala rufogularis* and *P. inornata* (Fig. 13). The former occupies a very restricted, and presumably specialized, area in the mallee of eastern South Australia — western Victoria. The latter has a wide range and extends well beyond the limits of the mallee.

(vii) *Acanthiza ewingi* — *A. pusilla* and *Pardalotus quadragintus* — *A. punctatus*, cases of double invasion of Tasmania. In each genus the earlier invader (the first named in each case) has the more restricted habitat and range as well as being the rarer form. Thus, *Acanthiza ewingi* is chiefly an inhabitant of the "deeper forests and scrub" and *Pardalotus quadragintus* has a very "patchy" distribution (Sharland, 1945). The later arrivals have a wider, more continuous range and generalized habitat requirements.

(e) Interspecific Competition and its Influence on Habitat Plasticity

This subject is to be treated in detail elsewhere, and hence will only briefly be reviewed here.

Two situations that have now been recognised in various parts of the world have a series of Australian parallels. These are:

(i) The occupation of broader habitat zones in regions where there is no closely related competitor or, as it is sometimes expressed, greater "ecological tolerance" in such situations.

(ii) The occupation of the same or equivalent niche by distinct species in different areas.

Quite exceptional examples of these are to be found in the isolated sclerophyll forests of southwestern Australia, a section of the continent that might be described as a "forest island." It has an "unsaturated fauna" with fewer than 70 per cent of the species that occur in an equivalent section of the southeast. Presumably this is because only a proportion of species ever succeeded in reaching there, although some secondary extinction cannot be overlooked. The genus *Climacteris* (tree-creepers) is represented in eastern Australia by three species, one inhabiting mountain sclerophyll, one lowland sclerophyll, and the third savannah country. Only one species occurs in the southwestern corner (*C. rufa*) and it occupies wet and dry sclerophyll and savannah woodland, extending into the mallee association. *Gerygone* (arboreal warbler) is represented by three species in the southeast of the continent (but one of these lives in rain forest, an association absent from the southwest). The other two inhabit sclerophyll forest (*G. olivacea*) and dry savannah (*G. fusca*), respectively. In the southwest, however, where only the latter occurs, it inhabits both associations.

The Meliphagidae are represented by less than half the number of forest species found in the southeast. There are several significant cases of change of habitat to fill vacant niches. *Lichera indistincta* and *Meliornis novaehollandiae*, mainly mangrove and "stunted heathland" species, respectively, in southeastern Australia, are forest dwellers here. *Meliphaga virescens*, a strictly dry country and desert species in the east, in the absence of such related species as *Meliphaga chrysops, M. fusca,* and *M. melanops,* is the common forest honeyeater in the southwest. A specialized nectar-feeding marsupial (*Tarsipes*), with elongated snout, tubular lips, and brush-tongue has developed in southwestern Australia, the only place where such an ecological form occurs. This may well have been associated with the paucity of nectar-feeding birds there (Meliphagidae, Loriinae).[1] Lastly, an interesting case of ecological shift occurs in the thornbills, *Acanthiza,* in southwestern Australia. Here, there are only three species instead of five in any equivalent section of the east . Of the latter, two are foliage feeders (*A. lineata* and *A. nana*), two are ground feeders (*A. chrysorrhoa* and *A. reguloides*), and one (*A. pusilla*) is an intermediate feeder. The foliage feeders are, however, absent in the southwest where one of the ground feeders, *A.* (*reguloides*) *inornata,* has largely adapted to the vacant niche.

These examples of ecological replacement and displacement reflect those recorded in the Galapagos islands (Lack, 1947) and Hawaiian Islands (Amadon, 1950b, p. 246), and elswhere.

A search of the Australian avifauna reveals a variety of instances of equivalent habitats being occupied by different species in various parts of the continent. These occur in genera that have geographically representative species, e.g. in the honeyeaters (*Meliphaga*), and in finches belonging to the genus *Poephila.* More striking cases, however, are to be seen relative to some of the more specialized ecological "niches," thus:

(i) Trunks and branches of trees. Over the bulk of the continent this food niche is occupied by members of two genera, the tree-creepers (*Climacteris*) and nuthatches (*Neositta*). The bills of these birds are long and straight for the extraction of insects and spiders from the cracks and fissures, and they have strong feet and claws for supporting themselves in vertical positions. Neither group occurs in Tasmania (though there are a few sight records of individual tree creepers). Here, a large billed honeyeater (*Melithreptus* (*gularis*) *validirostris*) spends much of its time searching the bark (Sharland, 1945). Again, in the dense rain forests of Cairns-Atherton, only one species

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[1] The southwest has however, a much larger number of *species* of nectar-bearing shrubs than the southeast. These may well provide a more consistent nectar-flow from month to month and hence it may be this that has permitted the development of a specialized nectar-feeding marsupial.

of *Climacteris* occurs, *Neositta* being absent. A flycatcher, *Arses kaupi*, has here developed the habit of hunting over the trunks for insects.

(ii) Masses of eroded rock in gorges, in which fissures and caves occur. This niche might be typified by that of the cave-warbler, *Origma rubecula*, endemic to the sandstone-limestone area near Sydney, which finds its insect food about the rocks. In the Macdonnell Ranges in central Australia, however, a grass-wren, *Amytornis textilis*, has the same habits and food niche, and in northern Australia members of the *A. striatus* group behave in the same general way. In the Carnarvon Ranges of central Queensland, an area of sandstone similar to that near Sydney, the scrub-wren *Sericornis frontalis*, passingly utilizes the vacant niche.

Adaptations such as those outlined in this section stress the great versatility and adaptability of many birds with respect to habitat. They indicate how the ecological changes associated with adaptation to a new habitat coincident with speciation may be made. The competition of closely related species may, moreover, serve to consolidate habitat differences.

XIII. CONTINENTAL AND ARCHIPELAGO SPECIATION COMPARED

Quantitative Differences between Continent and Archipelago

The 425 bird species covered in the survey, only 70 of which actually range beyond the continent to any degree, have a total of 485-505 morphologically differentiated isolates in the section to the east of Wallace's Line (Timor, Palau, Samoa and New Zealand), and 211-226 isolates within Australia (Table 3). For a comparison of the ''potential'' of an archipelago and a continent for giving rise to new species, however, an area of the southwest Pacific of equivalent size to that of Australia, and which excludes New Guinea (that has partly a ''continental-type'' of speciation) must be taken. Such is shown in Figure 28. It embraces the Bismarks, the Gilberts, Solomons, Fiji, New Hebrides, and New Caledonia.

The bird species (53) occurring both in this area and in Australia, and the number of morphologically differentiated isolates in each, are set out in Table 10. The number of isolates in the island section is 201 and that on the continent 38-43; the island segment, significantly enough, has some five times as many. Several of the species, moreover, have an exceptionally large number of isolates in the archipelago region. Thus, *Accipiter novae-hollandiae* has 9; *Rallus philippensis,* 12; *Halcyon chloris*, 26, *Coracina tenuirostris,* 10; *Rhipidura rufifrons,* 18; *Petroica multicolor,* 10; and *Pachycephala pectoralis,* 34. These substantially account for the greater number of differentiated forms in the Pacific area. That the trend is, however, a general one is shown by the fact that only in three species does the number of continental isolates exceed the archipelago ones: *Butorides striatus*, *Turnix varia*, and *Rhipidura fuliginosa.* The last two of these extend for only a short distance into the archipelago area.

Fig. 28. Australia and an archipelago area of equivalent size in the southwest Pacific (enclosed by plain line) to compare potential for giving rise to new species.

Qualitative Differences between Continent and Archipelago

Since the days of Darwin and Wallace workers have been impressed by the striking and often bizarre appearance of insular races and species. This not only applies to the more isolated archipelagos like the Galapagos and Hawaii but is seen, to a degree, over a wide section of the southwest Pacific. The studies on *Rhipidura rufifrons* (Mayr and Moynihan, 1946), *Petroica multicolor* (Mayr, 1934), *Artamus leucorhynchus, Lichmera indistincta,* and others may be noted in this regard. It also often applies in the case of islands lying offshore from a larger land mass, as in the genus *Tanysiptera* in the New Guinea region (Mayr, 1954b). Bird species that do not vary at all on the Australian continent may have distinct populations on peripheral islands, e.g. *Dicaeum hirundinaceum, Poephila guttata.* Compared to many of these insular forms, continental variation is commonly minor and insignificant — an observation that, as noted, led Goldschmidt (1940) to believe that evolutionary processes on the two were dissimilar.

Archipelago and insular bird populations are commonly characterized by: (a) Marked shifts in colour pattern and in the distribution of body colour. (b) Shifts in the degree of sexual dimorphism within species. (c) Changes in the size and form of appendages, especially the bill and tail. (d) Changes in over-all body size.

The present survey reiterates the greater prominence and frequency of these changes under archipelago conditions. It also shows, however, that:

(a) All these different kinds of variation occur, to a degree, on the Australian continent. Marked shifts in colour pattern are typical of isolates of long-standing, e.g. as between the southeastern and southwestern populations of the finch superspecies *Zonaeginthus bellus* and the honeyeater *Acanthorhynchus tenuirostris.* Shifts in the degree of sexual dimorphism are minor and rare but occur in the whistler *Pachycephala pectoralis,* some of the wrens (*Malurus*) and as between species of the bower-bird genus *Chlamydera.* There is a marked case in the *Petroica cucullata-vittata* group but in this case Bass Strait has been the isolating barrier. Changes in bill-form in association, apparently, with a change from insect to seed-feeding, occur in *Amytornis* and *Turnix,* whilst a noticeable elongation of bill is seen in the case of certain nectar-feeding honeyeaters. For example, note the difference between the generalized bill of *Meliphaga fusea* and the elongated one of *M. macleana* (figured in Keast, 1959e). Differences in body size between closely related members of a genus are not common but do occur in *Amytornis.* Within species, continental size variation typically takes the form of a south-north cline of decreasing body size.

The trend is accentuated, with individuals from the southernmost and northernmost areas averaging a difference in size of 20 per cent or more, when the end populations are isolated from each other, e.g. in *Scisura inquieta* and *Megaloprepia magnifica.*

(b) Much of the archipelago and insular variation is also only minor. The more striking forms are, on the whole, in the minority.

Notwithstanding the above, it is a reasonable assumption that the small insular populations, morphologically distinctive though they may be, are over-specialized. They would probably have little future in the event of a marked change in their biotic environment, or were they introduced to the competitors and predators of a continent. It is with the generalized and versatile continental populations that the real future of each evolutionary line lies.

Comparison of the Continent and Archipelago as a Physical and Genetic Environment

Tropical and subtropical archipelagos differ from continents in various ways. Rainfall tends to be regular, if seasonal. Temperatures are equable. The rigorous climate that necessitates extensive latitudinal migrations or nomadic movements is lacking. There is necessarily a year-round supply of food available. The shore line sharply limits the range.

Archipelagos also differ from continents in that, resulting from the reduced opportunities for dispersal, they have only a fraction of the animal and plant species. A corollary is that potential food niches are likely to remain unoccupied on remote islands, simply because the right species are unable to reach them. This means, of course, that species are less likely to be confined, by competition, to a restricted way of life but can more easily diversify or become modified to a new niche. More strikingly, this same absence of competition has permitted and encouraged the bizarre radiation by the members of single groups that occurs on the Galapagos and Hawaiian islands.

The big problem in archipelago speciation is to explain how so many distinctive forms can develop on adjacent islands when, as environments, they are apparently similar. This was a subject that much occupied the mind of Darwin (1890, p. 355) and he sought to explain it away in terms of the biological, not the physical environment, thus: "How has it happened in the several (Galapagos) islands situated within sight of each other, having the same geological nature, the same height, climate, etc., that many of the immigrants should have been differently modified, though only a small degree. This long appeared to me a great difficulty; but it arises in chief part from the deeply-seated error of considering the physical conditions of a country as the most important for its inhabitants; where it cannot be disputed that the nature of the other inhabitants with which each has to compete is at least as important, and generally a far more important element of success.''

Mayr (1947), in quoting Darwin, stresses that individual islands in an archipelago are not as similar as they might at first appear but may differ in size and elevation, temperature and precipitation, ocean currents and, since their population by fauna and flora is fortuitous, as biotic environments.

Amadon (1950b) in a review of the remarkable modifications in the bill form of the Hawaiian honey-creepers comments on ''rapid divergent evolution'' in archipelagos and quotes Simpson's views that ''quantum evolution'' is associated with a change from one ecological niche to a radically different one. Such an explanation, however, can hardly account for the lesser changes in colour and colour pattern that characterizes so many of the insular forms in the southwest Pacific. Nor, since few of the populations are very small, is genetic drift (the fixation of hitherto neutral or unfavourable genes merely by chance) likely to play a major role.

An interesting theory has recently been advanced by Mayr (1954b) to account for the accelerated variation and differentiation in animal populations on islands adjacent to continents. This is, in effect, that insular populations, by nature of the fact that their founders could only possess a limited proportion of the gene reservoir of the species, have a different genetic ''environment'' than their parental forms. An all-important factor in the transition from one well integrated and conservative condition, through a highly unstable period, to another new period of balanced integration, lies in what genes are carried to the new areas by the founders. That the new complex will be different is assured by the following considerations: (a) As noted, the founders represent, genetically, only a segment of the parental variability; (b) alleles that had been previously of equal viability are likely to change their relative viability during the period of rapid readjustment; (3) recessives will have a much greater chance to become homozygous in the reduced population and thus become more exposed to selection.

XIV. SUMMARY

(1) The present study is a detailed investigation of species-formation in the Australian avifauna. It covers 425 (80%) of the 531 species of breeding land and freshwater birds occurring on the continent.

(2) Monotypic species (that do not vary geographically) amount to 188 (44%), whilst 99 (23%) have clinal variation only. Those with morphologically differentiated isolates on the continent total 138 (33%).

(3) The number of morphologically differentiated isolates, forms with the "potential" of developing into new species, totals 211-226, an average of 0.5 per species for the whole fauna, or 1.6 per species for the 138 that have them. Sixty (23%) of the isolates have differentiated to a marked or moderate degree.

(4) The continent is rich in demonstrations and examples of currently occurring speciation. Ten families provide examples of the full range of intermediate stages from isolated populations that have not yet differentiated to markedly different isolates and examples of range overlap, without interbreeding, of newly-evolved forms. An additional 8 families show examples of all stages but the last.

(5) Almost one-third of Australian bird species belong to superspecies. Many of these superspecies groups are entirely confined within the continent. There are about a dozen current cases of range overlap by newly evolved species, and about the same number of instances of (current) speciation by double invasion. (There are also various instances of successive invasion of an area by infraspecific forms.) Most of these invasions are from New Guinea to Australia and from the mainland to Tasmania. There is one good case of speciation by circle formation, with the end-members of a chain of forms infertile.

(6) The habitat (vegetation formation) occupied by a species, and the nature of a species' seasonal movements, individually exercise a strong influence on its potential for giving rise to isolates and hence new species. The family grouping to which it belongs, however, appears to have little influence, other than through what might be called the "ecological attributes" of that family. Of the total isolates in Australian birds, 14 per cent are to be found in species that are basically inhabitants of rain forest, 33 per cent occur amongst the sclerophyll forest dwellers, and 20 per cent belong to savannah woodland species.

much speciation occurring as between (i) the rain forest segments of Cape York, Cairns-Atherton, and south Queensland- These vegetation formations are peripheral in distribution and are broken up into isolated tracts. In contrast to this, few isolates occur in species specialized for life in the interior, continuously ranging, vegetation formations.

Nomadic bird species, amounting to some 23 per cent of the whole avifauna, have only an insignificant number of morphologically differentiated isolates. The overwhelming majority of isolates occur in the sedentary species. Virtually no isolates occur in the hawks and large water birds, which species are typically nomadic.

(7) The geographic isolating barriers leading to isolation and differentiation are discontinuities in the basic habitat (vegetation formation) of species. These are either tongues of dry or arid country that extend from the interior to the sea to break up the forested areas, or are tracts of sea. The way in which these barriers operate is discussed in detail. There is New South Wales, respectively, (ii) the sclerophyll forest tracts of southeastern Australia, Tasmania, and southwestern Australia and, (iii) the savannah woodland tracts of northwestern and eastern Australia. Differentiation is common between populations of species on either side of Torres Strait. It sometimes occurs on offshore islands. Further afield, a variety of Australian species have distinctive populations or counterparts in New Zealand, Lord Howe Island, and New Caledonia. Others have given rise to many insular forms in the archipelago areas of the southwest Pacific.

(8) The present study discloses the existence of about 33 hybrid zones, representing the premature re-uniting of differentiating forms. Most result from a minor climatic improvement that has permitted forms to spread out. The clearing of the forests has been a relevant factor in other cases. The geographical position of the various hybrid zones is discussed, it being pointed out that most occur between the main centres of isolation and differentiation (i.e., "refuge areas").

(9) The Australian climatic and physiographic environment of the Tertiary, Pleistocene, and early Recent, are reviewed. Much of the original radiation and speciation in birds took place under conditions of generalized fertility. Present-day aridity is a relatively recent development. The circumstances of Tertiary speciation cannot be seen. During the Pleistocene,

however, successive eras of range extension and isolation must have accompanied the periodic climatic shifts of the period. The "refuge area" type of isolation of today possibly occurred to a degree previously. The position of the refuges, peripheral mountainous or hilly areas, would have been the same because there has been virtually no mountain-building since the end of the Tertiary.

Since the distribution, and composition, of the basic vegetation formations (that compose the bird habitats) are dependent on the soil substratum, as well as rainfall, it is not valid to assume that any particular shift in the rainfall belts would alter the habitat distribution to the same degree. The soil itself is an evolving system. In the ultimate degree, the birds (their distributions and adaptations), the vegetation formations and their individual members, the soil, and the climate are all changing, individually and relative to each other. Nevertheless, through the habitat, rainfall and soil changes have a direct influence on bird distribution and speciation.

Colonization from, and by way of, New Guinea, and subsequent differentiation in Australia, have made a significant contribution to the building-up of the Australian avifauna, not only in recent times, but throughout geological history.

(10) "Ecological" speciation, the development of habitat differences between species, is reviewed in some detail. Cases of geographic variation in habitat occupied and habitat "differentiation," under circumstances of isolation, are discussed. It is noted that where marginal overlap and double invasion occur the two species separate out into slightly different habitats, notwithstanding that they occupy similar habitats elsewhere in the range. Likewise, species tend to occupy much broader niches where there is no competitor.

(11) Differentiation and speciation on the Australian continent is compared with that occurring in an archipelago segment in the southwest Pacific of equivalent size. It is found that there are five times as many morphologically differentiating isolates in the latter. Though much of the insular isolation is minor, studies on species like *Rhipidura rufifrons* and *Petroica multicolor* reiterate that insular populations tend to be subject to more marked shifts in colour pattern, in the degree of sexual dimorphism within species, and significant changes in size and form of appendages.

(12) To sum up, speciation is actively occurring in Australian

birds and the number of forms with the "potential" of developing into new species is large. All speciation is geographic. At the same time, the same basic factors and rules apply as in the island archipelago from which much of our basic knowledge of the speciation process has been built up.

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Additional field work has been carried out in Australia in the period 1955-1959. The costs of this were mostly borne by the Trustees of the Australian Museum. The Trustees of the Science and Industry Endowment Fund of the Australian Commonwealth Scientific and Industrial Research Organization were, however, kind enough to make me a grant to carry out my 1959 field work in Western Australia. Transport in central Australia in 1958 was kindly made available by the Director, and Mr. Alan Newsome, of the Animal Industry Division of the Northern Territory Administration. Dr. W. D. L. Ride, Director of the Western Australian Museum, Perth, kindly arranged for me to join his field party to the Barlee Range in 1959.

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TABLE 1

THE MAJOR VEGETATION FORMATIONS OCCURRING IN AUSTRALIA: THEIR CHARACTERISTICS

(Modified and enlarged from that in Wood (1949))

FORMATION	CHARACTERISTICS
Rain Forest	Dense assemblage of trees, canopy continuous, woody climbers (vines) present. Monsoon or pseudo rain forest, narrow strips of dense soft woods along the banks of rivers in parts of the northern coastal region, have a somewhat similar consistency.
Sclerophyll Forest	Trees of forest form, in closed community; dense undergrowth of hard leaved shrubs; grass rare. (Map groups wet and dry sclerophyll.)
Savannah Woodland	Rather open parklike communities of trees, with scattered shrubs and a few herbs. Grassy underfoot and with open areas.
Savannah Grassland	Grasslands with herbs and a few sub-fruticose shrubs, interspersed with a few trees, or small clumps of trees. Sometimes intermixed with tracts of savannah woodland.
Mallee Scrub	Associations of dwarf eucalypts, the trees characterised by multiple stems arising from a common base; growing in semi-arid regions frequently on soil with characteristic qualities (mallee soil). Growth is generally rather open. Scattered shrubs and tracts of clumped porcupine grass (*Triodia*) are present.
Mulga Scrub (desert steppe)	Small trees with dense or scattered shrubs, few herbs, and with vast tracts dominated by the Mulga (*Acacia ancura*).
Desert Grassland (desert steppe)	Sand-plain covered with tussocks and clumps of spiny sclerophyllous grass (sometimes fairly continuous, sometimes sparse), mainly spinifex or porcupine grass (*Triodia*). Chenopodaceous plants. Marked seasonal herbage after rains. Gibber desert, plains with gravel and stone pavement, vegetation minimal, is included here.
Mangroves	Shrubs or trees in littoral zone, growing in formations that may be relatively open or of dense and shady consistency.
Swamps, marshes and rivers	Areas of fresh water that are either open, associated with sparse trees, or densely covered with reed-bed.
Miscellaneous	Includes various minor subdivisions, e.g. rocky outcrops and river gorges.

TABLE 2

MAJOR VEGETATION FORMATION: AREA COVERED BY EACH, AND RICHNESS IN TERMS OF NUMBER OF BIRD SPECIES

Each bird species is included only once, it being placed under the formation to which it is confined or, in the case of those species that occur in more than one, under the formation that is judged to be its main habitat.

	HABITAT		BIRD SPECIES		
Type	Area in sq. miles	% of continental area	(Approx.) Number of species	% of total avifauna	Number of sq. miles of habitat/species
Rain forest	20,000	0.66%	81	16	247 (x)
Sclerophyll forest	210,000	7	86	16	2,500
Savannah woodland	720,000	24	? (148)	(28)	4,932
Savannah grassland	480,000	16	? (59)	(11.5)	8,135
Mallee	210,000	7	10	2	23,330
Mulga	900,000	30	? (24)	(4.5)	37,500
Desert grassland (spinifex) and steppe & gibber	420,000	14	17	3	24,705
Mangroves	Negligible (perhaps 1,000 sq.m.)	Negligible	16	3	70
Swamps & marshes	Negligible	Negligible	74	14	—
Miscellaneous	Negligible	Negligible	16	2.5	—
TOTAL (actual)	2,984,000		531	—	5,772

(x) A high proportion of the species confined to this habitat are New Guinea species that have colonized the continent in comparatively recent times.

TABLE 3

AUSTRALIAN BIRD SPECIES: SUMMARY OF GEOGRAPHIC VARIATION, ISOLATION AND SPECIATION TRENDS

In the column referring to the number of isolates beyond Australia the symbol "x" means that there is a solitary differentiated population beyond the continent, and "(x)" means that the species extends there without differentiation. In order to enable proper comparisons to be made, each species extending beyond the continent is regarded as having a "parental form" both inside and outside of the continent. That is to say, the "x"'s in this particular column are not included in the totals and subsequent calculations. All figures refer only to isolates in the section to the *east* of Wallace's Line.

In the sixth column, if the species is a member of a superspecies group centred to the *west* of Wallace's Line this is indicated by the symbol (or figure) being placed in brackets. Again these are not included in the totals.

TABLE 3 (Continued)

	MONOTYPIC (in Aust.)	POLYTYPIC				ISOLATES		HYBRID ZONES
Species	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differentiation	Slight Diffn.	
Fam: PODICIPITIDAE								
Podiceps cristatus	x			(x)				
P. novae-hollandiae		x		2	(x)			
P. poliocephalus		x						
Fam: ACCIPITRIDAE								
Elanus notatus	x							
E. scriptus	x				(x)			
Aviceda subcristata			1?	12	(x)		1	
Milvus migrans	x			(x)	(x)			
Lophoictinia isura	x							
Hamirostra melanosternon	x							
Haliastur sphenurus	x							
H. indus	x							
Accipiter fasciatus		x		6				x
A. cirrhocephalus		x		3				x
A. novae-hollandiae		x		19				
Erythrotriorchis radiatus	x							
Hieraaetus morphnoides	x			x	(x)			
Aquila audax			1	(x)	(x)		1	
Haliaeetus leucogaster	x			(x)				
Circus approximans	x			(x)				
C. assimilis	x							
Falco hypoleucos	x							
Falco subniger	x							

F. berigora		x		x	(x)			
F. peregrinus			1?	2	Cosmop		1	
F. longipennis		x			(x)			
F. cenchroides	x			1	(x)			
Pandion haliaetus		x		(x)	Cosmop			1
Fam: GRUIDAE								
Grus rubicunda	x				(x)			
Fam: ARDEIDAE								
Ardea sumatrana	x				(x)			
Egretta garzetta	x			x	(x)			
E. intermedia	x			x	(x)			
E. alba	x			1-2?	Cosmop			
Notophoyx novae-hollandiae	x			x				
Ardea pacifica	x			(x)				
N. picata	x			(x)				
Demigretta sacra	x			x				
Nycticorax caledonicus	x			3				
Butorides striatus			5	8	(x)	1	4	
Ixobrychus minutus	x			1	(x)			
Dupetor flavicollis	x			2	(x)			
Botaurus stellaris	x			(x)	(x)			
Fam: THRESKIORNITHIDAE								
Plegadis falcinellus	x			(x)	Cosmop			
Threskiornis aethiopica		x		(x)	(x)			
Carphibis spinicollis	x							
Platalea leucorodia regia	x			(x)	(x)			
P. flavipes	x							
Fam: CICONIIDAE								
Xenorhynchus asiaticus	x			(x)	(x)			

TABLE 3 (Continued)

	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
Species	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differentiation	Slight Diffn.	
			Fam: ANATIDAE					
Cereopsis novaehollandiae	x							
Anseranas semipalmata	x			(x)				
Cheniscus coromandelianus	x			(x)				
C. pulchellus	x			(x)				
Chenonetta jubata	x			(x)				
Chenopis atrata	x			(x)				
Dendrocygna arcuata	x			2	(x)			
D. eytoni	x			(x)				
Tadorna radjah	x			(x)	(x)			
Casarca tadornoides	x							
Anas superciliosa	x			1	(x)			
A. castanea	x			2				
A. gibberifrons	x			2	x			
Spatula rhynchotis	x			(x)	(x)			
Malacorhynchus membranaceus	x							
Stictonetta naevosa	x							
Aythya australis	x			x)				
Oxyura australis	x							
Biziura lobata	x							

		Fam: RALLIDAE					
Rallus pectoralis			1	2-3			1
Rallus philippensis			1	18			1
Eulabeornis castaneoventris	x			x			
Rallina tricolor	x			3			
Porzana fluminea			1				1
P. pusilla	x			x	(x)		
P. tabuensis	x		1	6	x		1
Poliolimnas cinereus	x			6			
Amaurornis olivacea	x			2-3			
Tribonyx mortieri	x						
T. ventralis	x						
Gallinula tenebrosa			1	2	(x)		1
Porphyrio porphyrio			2	8	(x)	1	1
Fulica atra	x				(x)		
		Fam: TURNICIDAE					
Turnix maculosa		x		1-2			
T. varia			3	x			3
T. castanota			1			1	
T. melanogaster	x						
T. velox		x					
T. pyrrhothorax			1?			1	
Pedionomus torquatus	x						
		Fam: COLUMBIDAE					
Ptilinopus regina			1	2-3	x	1	
P. superbus	x			(x)			
P. alligator	x				x		
Megaloprepia magnifica			2	2			2
Ducula spilorrhoa	x			1	x		
Lopholaimus							

TABLE 3 (Continued)

	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
Species	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differentiation	Slight Diffn.	
antarcticus		x						
Columba								
norfolciensis		x						
Macropygia								
phasianella			1	x	x		1	
Geopelia striata			1	3			1	1
G. cuneata		x						
G. humeralis		x		x				
Chalcophaps								
indica			1	4			1	
Phaps chalcoptera		x						
P. elegans		x						
Histriophaps								
histrionica	x							
Petrophassa								
albipennis	x				x			
P. rufipennis	x				x			
Geophaps scripta		x			x			
G. smithi	x				x			
Lophophaps								
plumifera			3-4			1	2-3	
Ocyphaps lophotes			1				1	1?
Leucosarcia								
melanoleuca		x						
Fam: PSITTACIDAE								
Trichoglossus								
moluccanus			1		x	1		
Opopsitta								
diophthalma			2	3		2		
Probosciger								

aterrimus	x			3				
Kakatoe								
roseicapilla		x						
Leptolophus								
hollandicus	x							
Larius roratus	x			6				
Geoffroyus								
geoffroyi	x			12				
Polytelis swainsoni	x							
P. alexandrae	x							
Platycercus elegans			2		x	1	1	H. with flaviolus
Platycercus								
flaveolus		x			x			3
P. caledonicus	x				x			
P. adscitus			?1-2				1-2	1
P. venustus		x			x			
P. eximius			1		x		1	1
P. icterotis		x			x			
Purpureicephalus								
spurius	x							
Barnadius								
barnardi			1		x	1		1
Barnardius								
zonarius			3		x	1	2	1
Psephotus								
haematonotus		x						
P. varius			1		x		1	
P. haematogaster			2			1	1	
P. pulcherrimus	x				x			
P. chrysopterygius			1		x	1		
Neophema pulchella	x				x			
N. splendida		x			x			
N. bourki	x							
N. chrysogaster	x							
N. chrysostoma	x							

Table 3 (Continued)

	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
Species	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differentiation	Slight Diffn.	
N. elegans			1				1	
N. petrophila			1				1	
Lathamus discolor	x							
Melopsittacus undulatus	x							
Fam: CORACIIDAE								
Eurystomus orientalis	x			x				
Fam: ALCEDINIDAE								
Alcyone azurea			1	1-2			1	
A. pusilla				1				1
Syma torotoro	x			3				
Dacelo novae-guineae			1?				1	
D. leachii			1	x			1	1?
Halcyon macleayi			1	1-2			1	
H. pyrrhopygius	x							
H. sanctus		x		3-4	x			
H. chloris		x		27	x			
Tanysiptera sylvia	x			x				
Fam: MEROPIDAE								
Merops ornatus	x							
Fam: MENURIDAE								
Menura novae-hollandiae			1?			1		
M. alberti	x							
Fam: ATRICHORNITHIDAE								
Atrichornis rufescens	x				x			
A. clamosus	x				x			

Fam: CAMPEPHAGIDAE								
Pteropodocys maxima	x							
Coracina novaehollandiae			2	2-3	x		2	
C. papuensis			2	9			2	
C. robusta		x						
C. lineata	x			10				
C. tenuirostris			1	18			1	
Lalage sueurii tricolor	x			x	x			
L. leucomela			2	9	x		2	
Fam: MUSCICAPIDAE Sub-fam: MUSCICAPINAE								
Rhipidura fuliginosa			5	7	x	1	4	1
R. rufifrons			1	20-21	x	1		
R. rufiventris		x		11	x			
R. leucophrys		x		1				
Seisura inquieta			2			1	1	
Piezorhynchus alecto			2	3		1	1	
Myiagra rubecula		x	1	1			1	
M. cyanoleuca	x			(x)				
M. ruficollis	x			x				
Machaerirhynchus flaviventer			1	2			1	
Arses kaupi	x				x			
Arses telescopthalmus	x			3	x			
Monarcha melanopsis		x		x	x			
M. frater	x			2	x			
M. trivirgata			1	10		1		
M. leucotis	x							
Microeca leucophaea			1	x			1	

Table 3 (Continued)

	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
Species	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differentiation	Slight Diffn.	
Microeca flavigaster			1	1			1	
M. brunneicauda	x				x			
M. griseoceps	x			2				
Petroica multicolor			1	12			1	
P. goodenovii		x						
P. phoenicea	x							
P. rosea	x				x			
P. rodinogaster	x							
P. cucullata		x			x			
P. vittata	x				x			
Eopsaltria australis			2			1	1	
E. georgiana	x							
Peneoenanthe pulverulenta		x		x				
Heteromyias cinereifrons	x				x			
Poecilodryas superciliosa			1			1		
Tregellasia capito			1		x		1	
T. leucops	x			6	x			
Tribe: PACHYCEPHALINI								
Pachycephala pectoralis			5-7	51+		2	3-5	
P. rufiventris		x		2				
P. rufogularis	x							
P. inornata			1				1	
P. lanioides			3			1	2	
P. olivacea			1?				1	

P. simplex			1	4		1	
Falcunculus frontatus			2			2	
Oreoica gutturalis		x					
Sub-fam: TIMALIINAE Tribe: CINCLOSOMATINI							
Sphenostoma cristatum		x					
Psophodes olivaceus		x			x		
P. nigrogularis			1		x		
Drymodes brunneopygia		x					1
D. superciliaris			1	2			1
Orthonyx temmincki	x			2			
O. spaldingi	x						
Sub-fam: SYLVIINAE							
Megalurus gramineus			2	x			2
M. timorensis	x			3-4			
Acrocephalus stentorius			1-2	1	(x)		1-2
Sub-fam: MALURINAE							
Epthianura albifrons			1				1
E. tricolor	x						
E. aurifrons	x						
E. crocea			3			3	
Ashbyia lovensis	x						
Gerygone olivacea			2	x		1	1
G. richmondi			2		x		2
G. palpebrosa			2	1-2		1	1
G. magnirostris-tenebrosa			1	7		1	
G. chloronota	x			1			
Gerygone							

TABLE 3 (Continued)

Species	MONOTYPIC (in Aust.)	POLYTYPIC				ISOLATES		HYBRID ZONES
	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differentiation	Slight Diffn.	
levigaster			2		x		2	
G. cantator	x				x			
G. fusca		x		1	x			
Smicrornis brevirostris		x						
Aphelocephala leucopsis			2				2	
A. pectoralis	x							
A. nigricincta	x							
Acanthiza lineata			1-2				1-2	
A. nana			2?				2	
A. inornata		x						
A. ewingi	x							
A. pusilla			4?			1	1	
A. robustirostris	x						4	
A. uropygialis		x						
A. iredalei			2					
A. reguloides			2?			1	1	
A. chrysorrhoa			2				2	
Acanthornis magnus	x							
Sericornis frontalis			1		x		1	1
S. maculata			3		x		3	1
S. humilis	x				x			
S. beccarii	x			7	x			
S. lathami			1				1	
S. magnirostris			1				1	
Oreoscopus gutturalis	x							
Pyrrholaemus								

brunneus	x						
Hylacola							
pyrrhopygia		x					
H. cauta			2			2	
Calamanthus							
fuliginosus			2	x		2	1
C. campestris			1	x		1	
Chthonicola							
sagittata		x					
Origma rubricata	x						
Pycnoptilus							
floccosus		x					
Eremiornis carteri	x						
Cinclorhamphus							
cruralis		x					
C. mathewsi		x					
Amytornis textilis			3	x	1	2	
A. modestus			1	x		1	
A. goyderi	x			x			
A. striatus			2	x	1	1	
A. woodwardi	x			x			
A. dorotheae	x			x			
A. housei	x			x			
Dasyornis							
brachypterus			1		1		
D. broadbenti			2		1	1	
Stipiturus							
malachurus			6	x	1	5	
S. ruficeps	x			x			
Malurus cyaneus			2	x		2	1
Malurus melanotus	x			x			
M. callainus		x		x			
M. splendens				x			
M. leucopterus			1		1		
M. lamberti			1	x		1	2
M. elegans	x			x			

Table 3 (Continued)

Species	MONOTYPIC (in Aust.) Variation nil.	Clinal Varn. only	POLYTYPIC No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	ISOLATES Marked to mod. Differ-entia-tion	Slight Diffn.	HYBRID ZONES
M. amabilis	x				x			
M. dulcis	x				x			
M. pulcherrimus			1		x		1	
M. melanocephalus			1				1	
M. coronata			1				1	
Fam: ARTAMIDAE								
Artamus leucorhynchus		x		7	x			
A. personatus	x							
A. superciliosus	x							
A. cinereus		x		1				
A. cyanopterus		x						
A. minor		x						
Fam: SITTIDAE								
Neositta chrysoptera			3	3	x		3	3?
Climacteris picumnus		x			x			
C. rufa			1		x		1	
C. melanura			1		x	1		
C. leucophaea			2	3	x	1	1	
C. erythrops		x			x			
C. affinis		x			x			
Fam: DICAEIDAE								
Dicaeum hirundinaceum		x		2-3	x			
Pardalotus punctatus			2		x		2	
P. xanthopygus	x				x			
P. quadragintus	x				x			
P. striatus		x						

P. substriatus		x						
P. melanocephalus			1·2				1·2	?1
P. rubricatus		x						
Fam: NECTARINIIDAE								
Nectarinaria jugularis	x			7				
Fam: MELIPHAGINAE								
Melithreptus lunatus			1		x	1		
M. affinis	x				x			
M. albogularis		x		(x)				
M. brevirostris		x						
M. gularis		x			x			1
M. validirostris	x				x			
Plectorhyncha lanceolata		x						
Myzomela dibapha		x		7	x			
M. erythrocephala			1	1	x	1		
M. pectoralis	x							
M. nigra	x							
M. obscura			1	5			1	
Certhionyx variegatus	x							
Acanthorhynchus tenuirostris			2		x		2	
A. superciliosus	x				x			
Gliciphila melanops		x						
Ramsayornis modesta	x			(x)				
R. fasciata		x						
Lichmera indistincta		x		5				
Grantiella picta	x							
Conopophila whitei	x							

TABLE 3 (Continued)

	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
Species	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differ-entia-tion	Slight Diffn.	
C. albogularis	x			x				
C. rufogularis	x							
Zanthomiza phrygia		x						
Glycichaera fallax	x			1-2				
Meliphaga lewini		x						
M. notata			1		x		1	
M. albilineata	x							
M. virescens		x			x			
M. versicolor	x			2	x			
M. fasciogularis	x							
M. frenata	x							
M. gracilis			1	1			1	
M. fusca		x						
M. chrysops		x						
M. flavicollis	x				x			
M. leucotis		x			x			
M. cassidix	x				x			
Meliphaga melanops		x			x			
M. cratitia		x						
M. keartlandi		x						
M. ornata		x						
M. plumula		x						
M. flavescens			2	x			2	
M. penicillata		x						
M. flava		x						
M. macleayana	x				x			
M. chrysotis	x			5	x			
Trichodere cockerelli	x							

Stomiopera unicolor		x						
Phylidonyris pyrrhoptera			2				2	
P. novae-hollandiae			1				1	
P. niger			1				1	
P. albifrons	x							
Manorina melanophrys		x						
Myzantha melanocephala		x						
M. flavigula		x			x }			
M. melanotis	x				x }			
Anthochaera chrysoptera			2			1	1	
A. carunculata			1		x }		1	
A. paradoxa	x				x }			
Acanthagenys rufogularis		x						
Entomyzon cyanotis			1	x		1		
Philemon novae-guineae			1	8+		1		
P. argenticeps		x						
P. corniculatus		x		x				
P. citreogularis		x		x				
Fam: ZOSTEROPIDAE								
Zosterops lateralis			3	6			3	2
Z. lutea			2		x		2	
Fam: PLOCEIDAE Sub-fam: ESTRILDINAE								
Estrilda temporalis			2				2	1
Zonaeginthus pictus	x							

TABLE 3 (Continued)

	MONOTYPIC (in Aust.)	POLYTYPIC				ISOLATES		HYBRID ZONES
Species	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differentiation	Slight Diffn.	
Z. bellus	x				x }			
Z. oculatus	x				x }			
Z. guttatus	x							
Poephila guttata		x		2				
P. bichenovii		x						1
P. phaeton			1	1		1		
P. ruficauda			1?				1	
P. cincta			former isol.		x }			1
P. acuticauda		x			x }			
P. personata			1			1		
Poephila gouldiae		x						
Erythrura trichroa	x			8	x			
Lonchura pectoralis	x							
L. modesta	x							
L. castaneothorax			?1	1	x		1	
L. flaviprymna	x				x			
Fam: ORIOLIDAE								
Oriolus sagittatus			1	x	x	1		
O. flavocinctus		x		x	x			
Sphecotheres vieilloti			1?	x			1	x
S. flaviventris		x		x				
Fam: DICRURIDAE								
Chibia bracteata	x			6				
Fam: EULABETIDAE								
Aplonis metallica	x			3				
Fam: CRACTICIDAE								

Strepera graculina				1		x	1		
S. fuliginosa		x				x			
S. versicolor				5		x	2	3	
S. arguta		x				x			
Cracticus nigrogularis			x						
C. quoyi				1	1			1	
C. torquatus				2			1	1	
C. mentalis		x			(x)				
Gymnorhina tibicen				1	x	x		1	
G. dorsalis		x				x			1
G. hypoleuca				1		x		1	
	Fam: GRALLINIDAE Sub-fam: GRALLINAE								
Grallina cyanoleuca		x							
		Sub-fam: CORCORACINAE							
Corcorax melanorhamphus		x							
Struthidea cinerea		x							
		Fam: PTILONORHYNCHIDAE							
Ailuroedus crassirostris				1	4-5		1		
Scenopoeetes dentirostris		x							
Ptilonorhynchus violaceus				1			1		
Chlamydera maculata				1			1		
C. cerviniventris		x			(x)				
C. nuchalis			x with step						1
Sericulus chrysocephalus			x						
Prionodura newtoniana		x							
TOTAL:	425	190	99	213-220	487-502	125(29)	59	154-161	33

TABLE 4

AUSTRALIAN BIRD FAMILIES: SUMMARY OF GEOGRAPHIC VARIATION, ISOLATION AND SPECIATION

FAMILY	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
	Variation nil	Clinical Varn. only	Number of isolates in Aust.	Number isol. beyond Aust. (est.)	Member of Super-species	Marked to mod. Diffn.	Slight Diffn.	
Podicipitidae 3, (3)	1	2		2	(1)			
Accipitridae, Falconidae, and Pandionidae 24, (24)	15	6	3	43	(8)		3	3
Gruidae 1, (1)	1				(1)			
Ardeidae 13, (13)	12		5	15-16	(7)	1	4	
Threskiornithidae 5, (5)	4	1			(2)			
Ciconiidae 1, (1)	1				(1)			
Anatidae 19, (19)	19			7				
Rallidae 14, (14)	9		7	47-49		1	6	
Turnicidae 7, (7)	2	2	5	1-2		2	3	
Columbidae 22, (22)	7	8	10-11	12-13	8	2	8-9	2
Psittacidae 30, (52)	15	6	17-18	24	14	8	9-10	8
Coraciidae 1, (1)	1							
Alcedinidae 10, (10)	3	2	4	36-39	2		4	2
Meropidae 1, (1)	1							
Menuridae 2, (2)	1		1			1		
Atrichornithidae 2, (2)	2				2			
Campephagidae 8, (8)	3	1	7	48-49	3		7	
Muscicapidae								
Muscicapinae 43, (47)	16	9	33-35	138-139	14	13	20-22	
Timaliinae 7, (10)	2	3	2	4	2		2	
Sylviinae 3, (5)	1		3-4	4-5	(1)		3-4	
Malurinae 69, (69)	25	10	61-62	17-18	28	14	47-48	5
Artamidae 6, (6)	2	4		8	1			

FAMILY	MONOTYPIC (in Aust.)		POLYTYPIC		ISOLATES			HYBRID ZONES
	Variation nil	Clinical Varn. only	Number of isolates in Aust.	Number isol. beyond Aust. (est.)	Member of Super-species	Marked to mod. Diffn.	Slight Diffn.	
Sittidae 7, (7)		3	7	6	7	2	5	3
Dicaeidae 8, (8)	2	4	3-4	2-3	4		3-4	1
Nectariniidae 1, (1)	1			7				
Meliphagidae 67, (67)	24	29	18	35-36	21	5	13	1
Zosteropidae 2, (2)			5	6	1		5	2
Ploceidae Estrildinae 18, (18)	8	4	6	12	7	2	4	3
Oriolidae 4, (4)		2	2		2	1	1	1
Dicruridae 1, (1)	1			6				
Eulabetidae 1, (1)	1			3				
Cracticidae 11, (11)	4	1	11	1	7	4	7	1
Grallinidae 3, (3)	3							
Ptilonorhynchidae 8, (8)	3	2	3	4-5		3		1
TOTAL 425	190	99	213-220	487-502	125(29)	59	154-161	33

The figures in the first column indicate the sample used in the present study, those in brackets the total number of species in each family in Australia. In addition, the following families and subfamilies of breeding land and fresh-water birds occur in Australia: Casuaridae, 1 species; Dromaeidae, 1; Phalacrocopacidae, 5, one of which is marine; Pelecanidae, 1; Megapodiidae, 3; Phasionidae, 3; Cuculidae, 11; Otidae, 1; Burtinidae, 1; Jacanidae, 1; Himantopidae, 2; Charadriidae, 5 (plus visitors); Glariolidae, 1; Recurvirostridae, 3; Scolopaciidae, 1; Laridae, 2, plus many marine species; Strigidae, 8; Aegothelidae, 1; Podargidae, 3; Caprimulgidae, 3; Apodidae, 1 (plus 2 migrants); Pittidae, 3; Alaudidae, 1; Hirundinidae, 4; Turdinae, 1; Corvidae, 3; Paradisaeidae, 3.

The figures in brackets in the sixth column refer to the number of species belonging to superspecies groups centered to the *west* of Wallace's Line.

TABLE 5
THE INFLUENCE OF VEGETATION FORMATION ON SPECIATION. ABSOLUTE FIGURES

HABITAT		MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYRID ZONES
	Number of species in sample	Variation nil	Clinal Varn. only	Number of isolates in Aust.	Number isol. beyond Aust. (est.)	Member of Super-species	Marked to mod. Differ-entiation	Slight Diffn.	
Rain Forest	70	34	9	31	177-183	20	13	18	—
Sclerophyll Forest	80	28	14	71-72	102-103	30 (1)	14	57-58	8
Savannah Woodland	113	32	43	61-64	91-95	32 (3)	19	42-45	18
Savannah Grassland	43	20	16	10	4	8 (4)	3	7	5
Mallee	10	5	2	4		4		4	
Mulga	15	7	8		1	2			
Desert Grassland (Spinifex)	15	9	1	8		10	3	5	1
Mangroves	16	8	2	10 11	52	13	2	8-9	1
Swamps	54	43	3	11-12	59-63	2 (20)	1	10-11	
Miscell. Habitats	9	4	1	7-8	1	4 (1)	4	3-4	
TOTAL:	425	190	99	213-220	487-502	125 (29)	59	154-161	33

In the seventh column the figures in brackets refer to the numbers of species belonging to superspecies groups centered to the *west* of Wallace's Line.

TABLE 6
THE INFLUENCE OF VEGETATION FORMATION ON SPECIATION. FIGURES EXPRESSED IN TERMS OF PERCENTAGES

HABITAT	MONOTYPIC (in Aust)		POLYTYPIC				ISOLATES		HYBRID ZONES
	Number of Species	Variation nil	Clinal Varn. only	Number of isolates in Aust.	Number isol. beyond Aust. (est.)	Member of Super-species	Marked to mod. Differ-entia-tion	Slight Diffn.	
Rain Forest	15	18	9.1	14	35.8	16	22	11.3	
Sclerophyll Forest	20	14.7	14.1	33.1	20.8	24	25	37.2	24
Savannah Woodland	28	17	43.1	30	18.8	25.6	32	28.4	54
Savannah Grassland	10	10.5	16.1	4.7	1	6.4	5	4.2	16
Mallee	2	2.6	2.1	1.7		3.2		2.4	
Mulga	3.4	3.7	8.1		.5	1.6			
Desert Grassland (Spinifex)	3.4	4.7	1.1	3.5		8	5	3.1	3
Mangroves	3.6	4.2	2.1	4.8	10.5	10.4	3	5	3
Swamps	12.5	22.6	3.1	5.1	12.4	1.6	1.4	6.2	
Miscell. Habitats	2.0	2	1.1	3.1	.5	3.2	6.6	2.2	
TOTAL:	100	100	100	100	100	100	100	100	100

Table 7

THE INFLUENCE OF SEASONAL MOVEMENTS ON SPECIATION

		MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
Category		Variation nil.	Clinical Varn. only	No. of isol. in Aust.	No. of isol. beyond Aust.	Member of Super-species	Marked to mod. Diffn.	Slight Diffn.	
Sedentary species	(294)	111	65	191-196	286-293	105 (10)	49	143-149	30
South-north migrants	(32)	10	11	15-17	119-125	10 (1)	5	9-10	—
Nomadic species	(99)	69	23	7	82-84	10 (18)	5	2	3
TOTAL:	425	190	99	213-220	487-502	125 (29)	59	154-161	33

In the sixth column the figures in brackets refer to the numbers of species belonging to superspecies groups centered to the *west* of Wallace's Line.

TABLE 8
ISOLATION AND SPECIATION ON OFFSHORE ISLANDS

Island	Distance offshore (miles)	Morphologically Distinctive Isolates
Tasmania (southeastern)	130. Longest water gap. 50	About 12 that have reached or are approaching the degree of differentiation typical of species, plus 20 lesser isolates.
King Island (southeastern)	50 from Tasm. 50 from Vict.	Minor forms of Melithreptus gularis, M. affinis, Acanthorynchus tenuirostris, Acanthiza ewingi, Malurus cyaneus (also on Flinders Island). Total: about 5.
Kangaroo Island (southern)	5-10	Minor forms of Melithreptus atricapillus, Anthochaera chrysoptera, Phylidonyris pyrrhoptera, Meliornis novaehollandiae, Acanthorhynchus tenuirostris, Meliphaga leucotis, Estrilda temporalis, Acanthiza pusilla, Stipiturus malachurus, Zonaeginthus bellus. Total: about 10.
Recherche Archipelago (southwestern)	5-20	Minor form of Sericornis maculata.
Abrollhos Islands (western)	40	Minor forms of Turnix varia, Sericornis maculata.
Dirk Hartog Island (western)	24	Malurus leucopterus (also on Barrow Is.). Minor forms of Calamanthus fuliginosus, Stipiturus malachurus.
Barrow Island (western)	35	Eremiornis carteri (minor form). An insular race of Anthus australis has been described from here.
Bernier Island (western)	20	Malurus lamberti minor form.
Melville Island (northwestern)	20	Minor forms of Turnix castanota (?), Coracina papuensis, Dacelo leachii, Meliphaga flavescens, Entomyzon cyanotis, Philemon novaeguineae, Myzomela obscura (?). Total: about 7.
Capricorn Islands (eastern)	25	Minor form of Zosterops lateralis.

TABLE 9

AVIFAUNAL RELATIONSHIPS BETWEEN AUSTRALIA AND THE MORE REMOTE SURROUNDING ISLANDS

	Species that have colonized Australia	Australian species that have colonized island
New Zealand	nil	8-10 in recent times (Falla, 1953), plus many older elements (Meliphagidae, Muscicapinae).
Lord Howe Island	nil	Up to about 10 (see Hindwood, 1940).
New Caledonia	nil	About 18 (see Mayr, 1945a).
Timor	20-22 (Mayr, 1944b)	About 17 (Mayr, 1944b).
New Guinea	66 plus	92 plus.

TABLE 10

CONTINENTAL AND ARCHIPELAGO SPECIATION. COMPARISON OF NUMBER OF MORPHOLOGICALLY DIFFERENTIATED ISOLATES IN BIRD SPECIES COMMON TO BOTH AREAS

Species	Number of Morphologically differentiated Isolates in southwest Pacific (Fig. 28)	Number of Isolates in Australia
Podiceps novae-hollandiae	2	—
Aviceda subcristata	4	1
Haliastur sphenurus	—	—
Haliastur indus	—	—
Accipiter novae-hollandiae	9	—
Accipiter fasciatus	—	—
Circus approximans	—	—
Falco peregrinus	1	—
Pandion haliaetus	1	—
Notophoyx novaehollandiae	—	—
Demigretta sacra	1	—
Nycticorax caledonicus	2	—
Butorides striatus	4	5
Dupetor flavicollis	1	—
Botaurus stellaris	—	—
Dendrocygna arcuata	1	—
Anas superciliosa	1	—
A gibberifrons	1	—
Aythya australis	—	—
Rallus philippensis	12	1
Rallina tricolor	2	—
Porzana tabuensis	—	1
Poliolimnas cinereus	4	—
Amaurornis olivaceus	1	—
Porphyrio porphyrio	5	2
Turnix maculosa	1	—

TABLE 10 (Continued)

Species	Number of Morphologically differentiated Isolates in southwest Pacific (Fig. 28)	Number of Isolates in Australia
Turnix varia	—	3
Chalcophaps indica	1	1
Trichoglossus haematodus	2	1
Eurystomus orientalis	—	—
Halcyon sanctus	2	—
Halcyon chloris	26	—
Coracina lineata	6	—
C. papuensis	5	2-3
C. tenuirostris	10	1
Lalage leucomela	5	2-3
Rhipidura rufifrons	18	1
R. leucophrys	1	—
R. fuliginosa	2	4-5
R. rufiventris	5	—
Piezorhynchus alecto	1	2
Petroica multicolor	10	1
Pachycephala pectoralis	34	5-7
P. rufiventris	1	—
Artamus leucorhynchus	4	—
Nectarinaria jugularis	1	—
Myzomela dibapha	—	—
Lichmera indistincta	1	—
Philemon novaeguineae	1	1
Zosterops lateralis	6	6
Erythrura trichroa	4	—
Chibia bracteata	2	—
Aplonis metallica	1	—
TOTAL	201	38-43

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